



---

## Searching for answers to the silent decline: first estimates of survival and recruitment for the critically endangered Rose's mountain toadlet, *Capensibufo rosei*

---

Francois Becker<sup>1</sup>

Supervisors: Dr Krystal A Tolley<sup>2</sup> & Dr Res Altwegg<sup>2</sup>

---

<sup>1</sup>*Department of Biological Science, University of Cape Town (UCT), Private Bag, Rondebosch 7701, South Africa*

<sup>1</sup>*Molecular Systematics Laboratory, South African National Biodiversity Institute, Kirstenbosch Research Centre, Private Bag X7, Claremont 7735 South Africa.*

<sup>2</sup>*Molecular Systematics Laboratory, South African National Biodiversity Institute, Kirstenbosch Research Centre, Private Bag X7, Claremont 7735 South Africa.*

<sup>2</sup>*Department of Statistical Science, University of Cape Town (UCT), Private Bag, Rondebosch 7701, South Africa*

In the submission of my Honthe s Thesis:

UCT Biological Sciences.

Email: [phogbecker@gmail.com](mailto:phogbecker@gmail.com)

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

## PLAGIARISM DECLARATION

1. I KNOW THAT PLAGIARISM IS WRONG. PLAGIARISM IS TO USE ANOTHER'S WORK AND PRETEND THAT IT IS ONE'S OWN.

2. I HAVE USED THE HARVARD CONVENTION FOR CITATION AND REFERENCING. EACH CONTRIBUTION TO,

AND QUOTATION IN, THIS THESIS FROM THE WORKS OF OTHER PEOPLE HAS BEEN

ATTRIBUTED, AND HAS BEEN CITED AND REFERENCED.

3. THIS THESIS IS MY OWN WORK.

4. I ACKNOWLEDGE THAT COPYING SOMEONE ELSE'S WORK, OR PART OF IT, IS WRONG, AND DECLARE THAT

THIS IS MY OWN WORK:

Signed: Francois Becker

Date: 31 Oct 2014

Signed by candidate

## ABSTRACT

*Capensibufo rosei*, a critically endangered bufonid found only within Table Mountain National Park, has shown a silent decline over recent decades, despite being found within a protected area with apparently pristine habitat. I estimated the first survival and recruitment rates for the species, using Capture-Mark-Recapture (CMR) methods, over a 7-year period, in order to identify demographic trends over time. I also used covariate models to test whether any observed trends in these demographic parameters were significantly related to variation in rainfall or drought-stress.

I found some evidence for an extreme rainfall-induced life-history plasticity, with both survival and recruitment rates covarying closely with rainfall parameters. Although recruitment rate showed a positive relationship with rainfall, the relationship between survival rate and rainfall, specifically during the start of breeding, was negative, with breeding season rainfall explaining 94% of the variability in survival rate over time.

I also found evidence to suggest that higher adult survival during poorer breeding rainfall years may be a natural population buffering mechanism to a highly variable microclimate, and that variable rainfall during the start of the breeding season may elicit a variable response in breeding investment by adults.

Finally, I found evidence to suggest that the population is small, range-restricted and highly unstable, and that disturbances at the breeding site during good breeding years may cause the population to crash.

## ACKNOWLEDGEMENTS

Many thanks to my supervisors, Dr Krystal A. Tolley and Dr Res Altwegg, for all their time and effort spent giving me guidance, reading through my drafts and questions, listening to my ideas throughout my thesis. Many thanks Dr G. John Measey, Dr Shelley Edwards, Dr Krystal A. Tolley and Paula Straus for their advice and guidance through my fieldwork, and their shared knowledge and experience on the species, and for the provision of their field notebooks and much of the data I used, and to Emily Cressey for the guidance I received from her MSc thesis. I also thank Thlou Manyelo, Tesray Linveeve, Hanlie Engelbrecht, and Tessa van der Lingen for their support and assistance in my fieldwork. Thank you to Thank you University of Cape Town (UCT), the National Research Fund (NRF) and the South African National Biodiversity Institute (SANBI) of the opportunity, resthe ces and funds provided to me to do this project. And finally, I want to acknowledge and thank the most important people in my life: God, my fiancé, Tessa van der Lingen, and my parents Richard and Elisabeth Becker, for all their love, support and help in life, and in getting me to the point of completion of this project.

**Cape Nature permit numbers:** 0035-AAA004-00322 (2009-2011);

0056-AA008-00021 (2013-2015)

**SAN-Parks permit:** Agulhas and Table Mountain National Parks, issued 06 February 2014 to Dr G. John Measey

**University of Cape Town ethical clearance numbers:** 2011/V16/EC; 2014/V9/RA

**South African National Biodiversity Institute ethical clearance number:** 001/10

## INTRODUCTION AND LITERATURE REVIEW

In the context of the on-going global biodiversity crisis, areas with high endemism and diversity have often been prioritised as inclusions in protected area networks (Brooks et al. 2006). However, simply creating protected areas may not be enough to ensure that the biodiversity they contain is conserved (Parrish et al. 2003). Many studies have shown that reserves may need to be closely monitored and management adapted accordingly, to ensure the natural ecosystem fluxes and processes remain intact (e.g. Bengtsson, Nilsson, Franc, & Menozzi, 2000; Grumbine, 1994; Kremen, Merenlender, & Murphy, 1994), particularly in the case of small reserves and reserves surrounded by development (Colding 2007; Kremen et al. 1994). In cases where ecosystem degradation may have already caused species declines, active management intervention may be needed to restore such species and their habitats (Foin et al. 1998). Hence, without active and informed management, ecosystem degradation and resulting species extinctions may continue within a protected area, despite efforts against direct habitat destruction (Colding 2007; Parrish et al. 2003).

The Cape Floristic Region in South Africa is regarded as one of the most diverse regions in the world, on both species and higher taxa levels (Cincotta et al. 2000; Cowling et al. 2003). It is also one of the regions with the highest levels of endemism in the world (Mittermeier et al. 1998; Myers 1990). Although the Western Cape flora is relatively well-studied, its highly endemic faunal assemblage has received considerably less attention in the literature. Table Mountain National Park (TMNP), established in 1998, and currently protects 265-km<sup>2</sup> of this endemic fynbos habitat on the Cape Peninsula. Much before its official recognition as a national park, a 300-km<sup>2</sup> area of Cape Peninsula Protected Natural Environment (CPPNE) had already been set aside (SANParks 2004, Wilgen et al. 2012). Table Mountain National Park is split into a number of smaller reserves, completely surrounded by urban development, agricultural land and ocean

(Richardson et al. 1996). Hence, ecosystem processes and functioning may be heavily influenced by human activities and by the changing land management practices within the park. For instance, pollution, urban noise and the constant presence of hikers and tourists – TMNP receives about 4.2 million visitors annually (SANParks 2004) – may all have negative impacts on certain sensitive species within the park. Management of natural fires through exclusion and changes in fire frequency in different areas of the park, may have markedly changed the natural disturbance regimes (Forsyth & Wilgen 1998; Wilgen et al. 2012). The historic removal or extinction of large ungulates, such as the quagga (*Equus quagga quagga*), Cape mountain zebra (*Equus zebra zebra*), kudu (*Tragelaphus strepsiceros*), eland (*Taurotragus oryx*), black rhinoceros (*Diceros bicornis*), African bush elephant (*Loxodonta africana*) and bontebok (*Damaliscus pygargus pygargus*) from the Peninsula (SANParks 2004), may also have changed the local ecosystem processes and fluxes, although the bontebok and eland have recently been reintroduced into the Cape of Good Hope section of TMNP. Furthermore, there have been large-scale invasions by alien vegetation in many regions of the park, both presently and in the past. Such anthropogenic-induced changes may have greatly altered the ecosystem function and morphology within the park (van Wilgen et al. 2008; Van Wilgen et al. 2010), and may threaten the biodiversity it supports. Furthermore, the amalgamation of multiple negative impacts decrease ecosystem resilience to climate change (McKinney 2002; Sauvajot et al. 1998; Liley & Clarke 2003), which may affect the more sensitive taxa first.

Amphibians are particularly sensitive to such habitat and climatic changes, and are thus the vertebrate taxon worst affected by the current biodiversity crisis (Beebee 2005; Stuart et al. 2004). According to the 2004 Global Amphibian Assessment of the IUCN, at least 43% of the 5 743 species known to science are declining, while 32% are threatened with extinction. About 113 species are thought to have gone extinct in recent decades, with at least nine confirmed extinct since 1980 (IUCN 2004).

Many amphibians have complex life-histories, with the different life stages having very different habitat requirements. Hence, amphibians often need a complex range of microhabitat types close together, and can lead to extreme habitat and niche specificity in some cases, which results in restricted and fragmented distributions (Baldwin et al. 2006; Turner & de Villiers 2007). Some amphibians also show high fidelity for a particular breeding site, which can further diminish population range (Shirose et al. 1997; Blaustein et al. 1994). According to the small population paradigm, small, range-restricted populations are more susceptible to the effects of random stochastic events, which may drive the population to extinction within a short span of time (Caughley 1994). Their life-history traits leave many amphibians sensitive to stressors in both terrestrial and aquatic habitat components, such as changes in landscape hydrology or water chemistry, as well as in vegetation structure or insect prey abundance (Blaustein, Belden, Olson, Green, Terry, et al. 2001). Furthermore, their dependence on moisture makes amphibians highly sensitive to changing patterns in rainfall and temperature (Blaustein, Belden, Olson, Green, Root, et al. 2001). Amphibians are often used as an indicator taxon for this very reason (Welsh & Ollivier 1998). Hence, monitoring amphibian populations within a protected area is not only a priority to ensure that they are successfully conserved, but can also give an indication of the overall ecosystem health and functioning, as a further measure of conservation success.

Many amphibian declines and extinctions have recently been recorded in relatively unperturbed habitats. These so-called “enigmatic declines” (Stuart et al. 2004) or “silent extinctions” (Hof et al. 2011) may be due to the wide range of possible stressors that may impact amphibian populations. It is often difficult to tease apart the important driving factors of such declines and the interactions between them, whether natural, climate-related or anthropogenic (Blaustein & Kiesecker 2002; Stuart et al. 2004).



A striking example of such a silent decline is that of Rose's mountain toadlet, *Capensibufo rosei*. This small bufonid is found only on the Cape Peninsula, within the Table Mountain National Park (Cressey et al. 2014). It lives and breeds in the indigenous mountain fynbos heathland in the national park (Measey 2011), although some of its former habitat may have been near or in what is now urban developments and heavily altered land (Cressey et al. 2014). The genus *Capensibufo* is endemic to the Western Cape mountain fynbos, and was originally divided into two species, *C. rosei* and *C. tradouwi*. However, recent phylogenetic work has identified a number of cryptic species within each (Tolley et al. 2010).

As a result of this phylogenetic work, the *C. rosei* on the Peninsula was elevated to a separate species, while the former *C. rosei* east of False Bay are considered *incertae sedis*, and are in need of taxonomic revision. Since this re-classification, *Capensibufo rosei* has been reassessed for the IUCN Red-list and the Critically Endangered status has been recommended (SAFROG, Pers. comm.). *Capensibufo rosei* has also been identified as one of the highest conservation priorities among South African frog species, regarding conservation research and management efforts (Measey 2011, Ch. 3, 4, 5).

There are currently only two known populations of *C. rosei*, both within TMNP. The one population breeds in the Silvermine section of TMNP (henceforth referred to as Silvermine), the other in the Cape of Good Hope section located near Cape Point (henceforth referred to as Cape Point). At least five historically known breeding sites were active during the 1900's, only one of which still remains active (Silvermine), while the population at Cape Point was only found in 2010. The two populations, approximately 20km apart, are genetically distinct with no shared haplotypes, suggesting no current or historical gene-flow between the two populations (Cressey et al. 2014). Although the Silvermine population shows genetic diversity similar to that of other amphibian populations, the Cape Point population shows very low levels of

genetic diversity (Cressey et al. 2014). This is considered a symptom of a small or declining population (Page & Holmes, 1998). Alternatively, it suggests that the population had gone through one or more bottle-necks (Garris et al. 2005; Hyten et al. 2006). The observed quantity of spawn and tadpoles at Cape Point was also initially very low compared to the Silvermine population (Cressey et al. 2014), although the quantity had increased since 2012.

Breeding takes place in small ephemeral pools or puddles, during the late winter rainy season, i.e. July to September (Measey 2011; Cressey et al. 2014). They are explosive breeders, and hundreds of male toads aggregate densely in the few breeding puddles, where they await the rarely encountered females, which generally only enter the puddles briefly to lay eggs. They often select shallow, exposed puddles with little or no water flow, where they aggregate and lay strings of eggs that sometimes exceed the volume of water (based on observations both at the two current breeding sites, as well as information on the historic breeding populations). The puddles generally dry up within a few weeks after the breeding had commenced. Adults return to the same breeding site, and often the same puddle to breed. This, together with the observed pattern of genetic isolation, suggests extremely high levels of philopatry regarding breeding site, poor dispersal ability, and a small range for the two populations. However, it is hard to determine the actual foraging range of the adults due to their cryptic nature (Cressey et al. 2014).

When considering that the reproductive output for each breeding population is contained within a few small puddles, and that, despite considerable efforts to locate other breeding sites, none have been found, this seems to indicate a very small population size in both cases. Furthermore, the observed number of adults at the two sites at any given time number in the hundreds at most, which is very little considering the small size of the animals and the available habitat space. With only two known

populations in existence for the species, both of them apparently small and range-restricted, and with the apparent disappearance of the fthe historic populations, the situation should be considered critical.

*Capensibufo rosei* is not only Critically Endangered, but also possesses many other “aspects of irreplaceability” (Brooks et al. 2006), which have been identified by numerous authors as priority criteria for conservation efforts: it is rare, regionally endemic, is unique taxonomically, it comprises part of an endemic and irreplaceable ecosystem type, and is a rare biological phenomenon: it the only voiceless anuran species in Southern Africa, and one of the few globally. It is even missing middle-ear components, and there is little concrete evidence to suggest how or why they aggregate in a particular puddle, without calling or hearing capabilities.

Although some information has been gleaned about the basic biology and life-history of this species, nothing is known about its population demographics. There have been no estimates for longevity, adult survival rates, recruitment rates or overall population stability, yet this information is crucial for understanding its conservation status (Measey 2011). It is currently unknown whether the two populations are stable or fluctuating, declining or increasing. Such demographic information will have management implications for the species, and research therein has been identified as a top priority regarding the conservation of the species, in an assessment of strategies for conservation research for South African amphibians (Measey 2011).

There is also little evidence to suggest why some of the historic breeding populations have disappeared, or what factors are currently influencing the surviving populations. Factors which may influence survival or breeding success include changes in: fire regime; vegetation or habitat structure; temperature and rainfall patterns; lack of natural disturbances for breeding sites; frequent human presence in and around the breeding sites.

Relating demographic trends to changes in environmental factors, specific events or changes in management strategies, will be the first concrete evidence towards identifying potentially important driving factors of decline. Such information can identify management practices which may mitigate further declines or improve population health. Research on potential driving factors of population trends has also been identified as a key area of conservation research for the species (Measey 2011). Furthermore, because *Capensibufo rosei* appears particularly sensitive to anthropogenic disturbance (Measey 2011), it is thus a valuable indicator of the health of the ecosystem it occupies. In essence, it can be considered an umbrella species for the native mountain fynbos ecosystem.

## **Aims and Hypotheses**

The main aims of this study are to provide the first estimates of survival and recruitment rates for the species, examine potential drivers of variation in these demographic rates, and to identify population trends over time. These demographic parameters were estimated using new and existing capture-mark-recapture (CMR) data.

### **Hypothesis 1:**

Phylogenetic evidence and general observations suggest that both populations are small and range-restricted. Small, restricted populations are more vulnerable to stochastic events and short-term environmental changes within the restricted range, and are thus unstable over time (Caughley 1994). Hence, I hypothesize that survival rate, recruitment rate and population size will fluctuate considerably within the seven-year study period.

#### Hypothesis 2:

Amphibians are highly moisture-dependent and easily desiccate because of sensitive, their porous skin (Hazell et al. 2003). Hence, I hypothesise that survival rate will relate positively to rainfall, and negatively to drought-stress factors (e.g. higher evaporation rates).

#### Hypothesis 3:

The breeding puddles are rain-filled, very shallow, and highly temporal. Hence, the developing eggs and tadpoles are highly dependent on rainfall and atmospheric conditions regarding during and before the breeding period. Furthermore, because of their reduced body size, new recruits would be more sensitive to prevailing environmental conditions than adults, even after the breeding period. Hence, I expect that recruitment rate will show a positive relationship with rainfall, but a negative relationship with drought-stress factors.

#### Hypothesis 4:

Because of a range of factors including predation and metabolism, smaller amphibians (and other animals) generally have shorter life-spans (Blanco & Sherman 2005; Morrison et al. 2004). Because of this, smaller animals are generally more R-selected and rely more on reproduction than on survival (Pianka 1970). Hence, I expected higher recruitment and lower survival rates, relative to one another.

# MATERIALS AND METHODS

## **Study site**

The two breeding populations are both located within the Table Mountain National Park (Fig.1). Because of the genetic distinction between the two populations, each population was treated as a separate site, with no migration considered between the two. The breeding population at Silvermine was monitored since 2007 (8 years of CMR data available), while the Cape Point site was only discovered in 2010 and monitoring began in 2011 (4 years of CMR data available). The Cape Point population had not yet been monitored for long enough to adequately examine the variation in survival or recruitment over time. For this reason, I concentrate on the Silvermine data for the rest of my thesis.

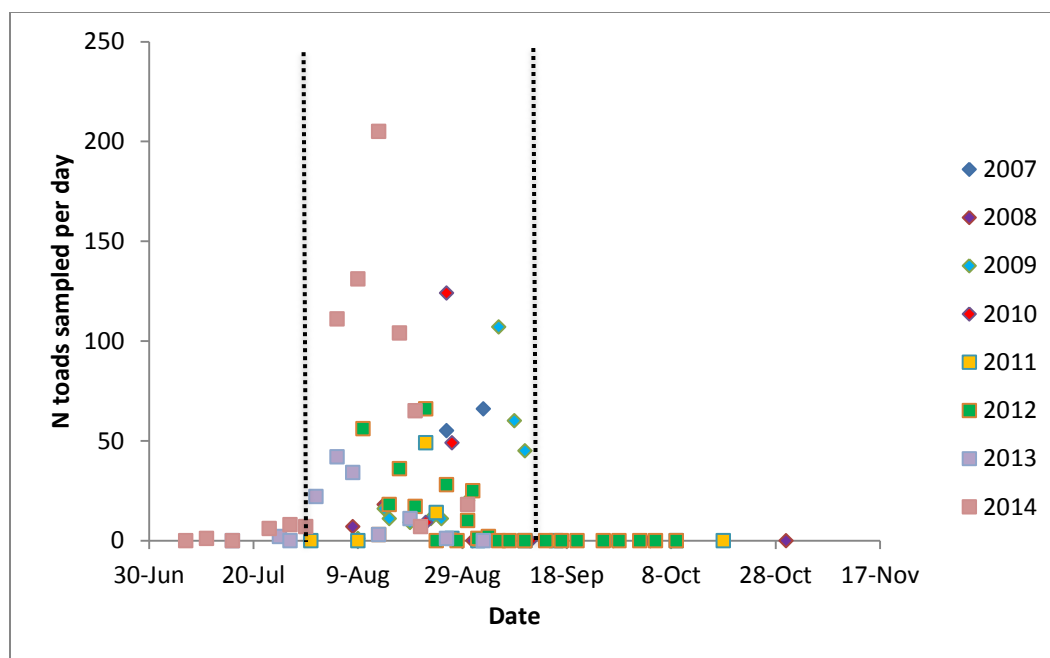
The breeding puddles at both sites were found in relatively exposed areas, with little vegetation other than short grasses and restios around or in the breeding puddles. The breeding puddles at Silvermine were often on the hiking path or road, while the entire breeding site at Cape Point was situated within a clearing consisting mainly of short grasses and restios, and often grazed by the resident bontebok and eland.



**Figure 1:** Approximate locations of current and historic breeding sites for *Capensibufo rosei* (Adapted from Cressey et al. 2014).

## Capture and processing

Because *C. rosei* is an explosive breeder like many other bufonids, capture and marking was performed during breeding events, when many toads could be captured within a single sampling session. They are hardly ever encountered during the rest of the year (Measey 2011). Furthermore, the statistical models used condition on short capture occasions (i.e. the short breeding period selected) relative to the period between occasions, in order to make more precise parameter estimations. During the breeding, sampling or capturing took place every 3-8 days, allowing time for the breeding to continue unperturbed between sampling sessions. The breeding period generally falls over two to three weeks, from July to the beginning of September (Fig. 2).



**Figure 2:** N toads sampled at the breeding site per sampling day over different sampling years, at Silvermine, South Africa. The general breeding peak is indicated between the two vertical dotted lines.



The CMR data were obtained through batch-marking by toe-clipping, which also doubled as a DNA sample. At first capture, all individuals received a year-specific batch mark/toe-clipping (Table 1). If marked from a previous year, the individual again received the year specific batch-mark of the particular year they were *recaptured* in, so that each toadlet essentially carries its capture history in the form of a combination of batch-marks. All missing toes that were within the recorded mark history (Table 1) were recorded as recaptures.

**Table 1:** Toe-clips or batch-marks for each sampling year, for the CMR analysis of *Capensibufo rosei*, Western Cape, South Africa

Year	Toe clipped
2007	Outer left
2008	Inner right
2009	Inner left
2010	2 <sup>nd</sup> inner right
2011	2 <sup>nd</sup> inner left
2012	3 <sup>rd</sup> right
2013	3 <sup>rd</sup> left
2014	Outer right

Captured toads were placed into a plastic container, sexed, measured, inspected for any missing toes (recaptures), and then marked (toe-clipped). The distal phalange of the selected toe was clipped. Individuals with deformed feet were not marked, and hence excluded from the CMR data. Tissue samples (toe-clips) were stored in 99% ethanol. Lengths were measured from snout to urostyle, to the nearest millimetre. Sex was determined by viewing the ventral surface of the animal. Male vents are usually more down-turned, possess a dark-colored double-swelling around the vent (Fig. 4), and

sometimes have a reddish glandular patch on the lower ventrum. Females have a less down-turned vent, without the dark swelling or the reddish glandular patch (Fig. 5). Females are often gravid with eggs (Fig. 7), or flaccid after egg-laying.

Finally, a photo was taken of all the toads from one puddle on laminated 1cm grid-paper, for record-purposes, and the photo number recorded. Then the toads were returned unharmed to the puddle or area they were removed from.



**Figure 4: Male ventrum**



**Figure 5: Female ventrum**



**Figure 6: Male toad**



**Figure 7: Gravid female toad**

## **Data analysis**

CMR data was analysed using program Mark (White & Burnham 1999). Mark not only estimates the demographic rates described below, but also calculates a confidence interval for each parameter estimate (Cooch & White 2014).

Because the sampled breeding sites are the only known breeding sites for the Silvermine population, the term “population” will henceforth be regarded as analogous with the terms “breeding site” or “sampling area”. The demographic models used do not discriminate between local survival and permanent emigration, or between local recruitment and immigration. However, because of the isolated nature of the breeding

site, I assumed that there was no significant migration into or out of the population when using the terms “survival rate” or “recruitment rate”, unless specified otherwise. Because the marks are annual batch-marks, data from all sampling days during the breeding period in a particular year, were pooled into one sampling occasion for the year. Hence, the term “sampling year” is analogous for “sampling occasion”.

### **Description of models:**

#### **(a) Survival Models (Live Encounter Models)**

The first set of models I used are the Survival Models, which are based on a standard Live Encounters Model (Cooch & White 2014). This model estimates two main parameters. The first is the **survival rate ( $\phi$ )**, which is the probability that an individual survives (or is still present in the population) from the initial sampling occasion (sampling year in this case)  $t_i$ , to the following sampling year  $t_{i+1}$ . The second is the **recapture rate ( $P$ )**, which is the probability that an individual captured in sampling year  $t_i$  will be recaptured in sampling year  $t_{i+1}$ , provided that it was still present and alive in the population at sampling year  $t_{i+1}$ . The basal model used was the fully time-dependent model,  $\phi(t) P(t)$ , whereby each of the parameters were allowed to vary fully with time ( $t$ ). The basal model was used for comparison of other models, and to identify the main trends in survival and recapture rate over time. I investigated whether the observed trends or fluctuations were related to any of the environmental covariates, by adding constraints (covariates) to the basal model, thus testing hypothesis 2. I used the best models to determine whether the survival rate fluctuates over short time-periods, shows longer-term trends or is stable over time, in testing of hypothesis 1. Recapture rate  $P$  was also constrained using different measures of capture effort and other covariates, to determine whether these caused significant variation in recapture rate. To describe the Survival Models, I used the short-hand model description format:

**$\phi(\text{covariate of } \phi)$   $P(\text{covariate of } P)$ .**

The Live Encounter Models use the entire recapture history after the initial encounter of an individual to estimate survival. Because these models separate the capture probabilities from survival, a low capture effort in a particular year will not reflect a false low survival rate, or vice versa. This makes these models much more robust than simpler CMR analyses, such as return rates, for example.

Assumptions of Live Encounter Models:

1. All marked animals alive in a particular year have the same probability of being recaptured.
2. All marked animals present immediately after the initial sampling occasion ( $t_i$ ), have the same probability of surviving to the following sampling occasion ( $t_{i+1}$ ).
3. All the marks are permanent; none were missed on captured animals.
4. All missing toes are marks or represent recaptures, provided that the toe had been clipped before the re-encountered occasion  $t_{i+x}$  (not lost due to natural causes).
5. Each release is made instantly after the capture, and each capture/recapture is instantaneous, relative to the interval between occasions ( $i$ ) and ( $i+1$ ).
6. Capture histories within each attribute group follow a multinomial distribution

I assessed whether the data met these assumptions by using goodness-of-fit (GOF) tests to verify the basal, fully time-dependent model  $\phi(t)P(t)$ . Subsequently, this model was used as a baseline for further model selection. Program program U-CARE (Choquet et al. 2009) was used for this GOF-testing.

GOF tests showed a lack of fit for the complete Silvermine dataset (program U-CARE, Tests 2 & 3 for live recaptures:  $\chi^2 = 46.2258$ ,  $df = 16$ ,  $P = 8.9836e-5$ ). After inspecting the

GOF results, I then identified the first cohort, individuals first marked in 2007, as potentially problematic, because recaptures of this cohort were very high in some years when the recapture probabilities seemed to be low for the other cohorts. This may have been linked to the particular toe that was removed in 2007, its identification in subsequent years (since it was a small toe relative to the others), or other unknown factors. Due to this, and because 2007 was the first sampling year, I decided to remove 2007 and all subsequent recaptures from this cohort, from the recapture histories. The resulting GOF tests indicated no evidence of lack of fit for the reduced data set (program RELEASE Test 2 cumulative:  $\chi^2 = 9.151$ ,  $df = 11$ ,  $P = 0.60796$ ) and thus little evidence for deviation of the data from following a multinomial distribution (Anderson et al. 1994). Hence,  $\phi(t) P(t)$  with 2007 cohort removed, was used as the basal model for further model comparisons.

#### (b) Pradel Seniority models

These models read the capture histories backwards in time to exploit the information in the data on when an individual entered the population, i.e. recruitment. The survival models condition on initial capture, so leading zeros in a capture history (noting the sampling occasions prior to the first capture on an individual) do not contribute to the likelihoods. In contrast, the Pradel models use the full capture histories. The Pradel seniority models estimate two main parameters: **Seniority rate ( $\gamma$ )**, which is the probability that an individual present in the population at  $t_{i+1}$ , was also present in the population at  $t_i$ , or the proportion of the population in a particular sampling year, which are survivors from the previous sampling year – the inverse of which are the proportion of new recruits in sampling year  $t_{i+1}$ . Secondly, it also estimates the recapture rate ( $P$ ), as in the survival models (a). I used the seniority models as a basis for selecting the most important covariates of recruitment for use in the combined survival and recruitment

models (c) described below. These covariate models were used to test hypothesis 3 (whether rainfall relates positively, or drought-stress negatively to recruitment rate).

Apart from the assumptions applicable to the Live Encounter Models (see above), the Pradel Models also assume that an animal can enter the population on any sampling occasion. However, since no effective GOF tests are available for these models (Cooch & White 2014), I used the same dataset as in the Live Encounter Models (combined sex recapture histories with cohort 2007 excluded from the dataset). The basal seniority model used was a fully time-dependent model  $\gamma(t) P(t)$ , i.e. both parameters allowed to vary fully with time. I then added constraints to the basal model to investigate if the observed trends in seniority rate were related to any of the environmental covariates (to test hypothesis 3), and to guide model selection for the combined survival and recruitment models (c) described below. The format used to describe the Seniority models, similar to before, is:

**$\gamma(\text{seniority constraint}) P(\text{recapture constraint})$**

#### (c) Pradel Survival and Recruitment Models

The third set of models used was the combined Pradel survival and recruitment models, which estimate three main parameters: survival rate ( $\phi$ ), recapture rate ( $P$ ), and **recruitment rate ( $F$ )**, which is the number of new arrivals/recruits in the population at  $t_{i+1}$ , per animal originally present in the population at  $t_i$ . These combined Pradel models read the capture histories in reverse (as described in (b) above) to estimate recruitment rate, but also read the data forwards in time to estimate survival rate (while  $P$  is estimated using a combination of the two). The format used to describe the Seniority models, similar to before, is:

**$\phi(\text{survival constraint}) P(\text{recapture constraint}) F(\text{recruitment constraint})$**

I used the combined survival and recruitment models primarily to investigate the trends and fluctuations in recruitment over time (to test hypotheses 1 and 3), using the basal, fully time-dependent model, as well as the AIC-best covariate models. I also used these models to derive estimates of the **population growth rate ( $\lambda$ )**, which is the proportional increase in size of the population from occasion  $t_i$  to occasion  $t_{i+1}$ . In other words,  $\lambda=1.5$  means that the population grew 1.5 times between  $t_i$  and  $t_{i+1}$ . Growth rate was derived from the parameters  $\phi$  and  $F$ , according to the following relationship:

$$\lambda_i = \phi_i + F_i$$

Furthermore, I used the estimates of growth rate to show the trend in the relative **population size** over time, to investigate the overall population trends and health. I was thus able to show the relative importance and contributions of recruitment and survival to the overall population size and growth (Nichols et al. 2014), to test hypothesis 4.

For survival and recruitment models, the first recruitment rate is confounded with the first capture probability and the last survival estimate is confounded with the last capture probability. Hence neither parameters are estimable, and were excluded from the graphs (Figs. 15 & 16). For the same reason, the last and first growth rates (Fig. 17) were also not estimable.

### **Model selection criteria**

The most parsimonious model, or model that best fits the structure of the data, which is the best-balanced model between an under-fitted (thus biased) or over-fitted (thus losing precision) model, is the model with the lowest AICc (Anderson & Burnham 2002; Altwegg et al. 2003). I used this to determine the most important covariates (or model constraints, Table 2) on survival rate ( $\phi$ ), seniority rate ( $\gamma$ ), and recruitment rate ( $F$ ).



I also used the analysis of deviance method (Skalski, Hoffmann & Smith 1993) to calculate the amount of variation in survival or recruitment rate explained by the important covariates, for the AIC-best models. This method follows the equation:  $V$  (proportion of total variance explained over time) =  $[\text{deviance}(\text{constant model}) - \text{deviance}(\text{covariate model})] / [\text{deviance}(\text{constant model}) - \text{deviance}(\text{time-dependent model})]$ .

### **Model covariates and interpretation**

To test hypotheses 2 and 3, one or more of the different parameters ( $\phi$ ,  $P$ ,  $F$  or  $\gamma$ ) of each of the different model types used (a, b and c above), were constrained using particular covariates (as summarised in Table 2), to test whether these covariates had a significant relationship with any of these model parameters.

When constraints are added to the survival rate  $\phi$  between two particular sampling years,  $t_i$  and  $t_{i+1}$  (e.g. 2008 and 2009), the variable from year  $t_i$  (2008 in this example) was used, because only variables prior to  $t_{i+1}$  can affect the survival rate during this period. Regarding recapture rate  $P$  between any  $t_i$  and  $t_{i+1}$ , I used variables from year  $t_{i+1}$ , because variables during this year, the year of *recapture*, would influence the probability of recapture. For recruitment rate  $F$ , the covariate from sampling year  $t_i$  was used, same as for the  $\phi$ -parameter constraints, because only parameters prior to recruitment can affect recruitment rate. However, this assumes that toads reach sexual maturity at 1 year of age. Although this information is not available for the species, the assumption is likely due to the small size of the toads, the range of sizes found at the breeding puddles and the annual breeding pattern. To assess the possibility of a bi-annual recruitment pattern (recruits which take 2 years to reach maturity/arrive to breed), I also fitted covariates from two years before  $t_{i+1}$ , or year  $t_{i-1}$ . However, as none of these models were well-supported by the data, I excluded them from the data analyses.

**Table 2:** A brief description of the different covariates used to constrain different model parameters in the capture-mark-recapture analysis of survival and recruitment of Rose’s mountain toad at Silvermine, South Africa. Survival rate is denoted as  $\phi$ , recapture rate as  $P$ , and seniority rate (proportion of sampling year  $t_{i+1}$  population that are survivors from the previous sampling year  $t_i$ , the inverse of which is proportion of new recruits in  $t_{i+1}$ ) as  $\gamma$ . All covariates used to constrain survival rate  $\phi$ , were used to test Hypothesis 2: that survival rate would relate positively to rainfall but negatively to drought-stress factors. All covariates used to constrain seniority rate  $\gamma$ , were used to test Hypothesis 3: that recruitment rate would relate positively to rainfall and negatively to drought-stress factors. Although not shown in this table, the covariates from the AIC-best seniority models were also used to constrain recruitment rate  $F$ , in the combined survival and recruitment Pradel models (Table 5). The covariates used to constrain recapture rate  $P$ , were used to test whether the observed trends in survival, seniority rate or recruitment rate over time are affected by capture effort or environmental factors which may influence the recapture rate, and thus affect the survival or recruitment rate estimates.

Constraint	Description	Parameter constrained
Total annual rainfall ( <b>train</b> )	Total annual rainfall (mm)	$\phi$ $\gamma$
Breeding season rainfall ( <b>brain</b> )	Mean monthly rainfall (mm p.m.) during July and August	$\phi$ $P$ $\gamma$
Development rainfall ( <b>drain</b> )	Mean monthly rainfall (mm p.m.) from August to October	$\gamma$
VPD maximum ( <b>vdpdmax</b> )	Highest monthly mean Vapour Pressure Deficit (VPD p.m.) for the year (Jan-Dec)	$\phi$ $\gamma$
Annual Maximum VPD ( <b>dvpdmax</b> )	Highest monthly mean VPD (p.m.) during larval development (Aug-Oct)	$\gamma$
Total pp-e ( <b>tpp-e</b> )	Net atmospheric moisture deposition/precipitation minus evaporation (mm) for the year (Jan-Dec)	$\phi$ $\gamma$
Breeding season pp-e ( <b>bpp-e</b> )	Net atmospheric moisture deposition (mm) during the start of breeding (Jul-Aug)	$\phi$ $\gamma$
Annual minimum pp-e ( <b>pp-</b>	Lowest monthly mean net	$\phi$ $\gamma$

<b>emin)</b>	atmospheric moisture deposition (mm p.m.) for the year (Jan-Dec)	
Development pp-e minimum ( <b>dpp-emin</b> )	Lowest monthly mean net atmospheric moisture deposition (mm p.m.) during larval development (Aug-Oct)	γ
Sampling people ( <b>ppsd</b> )	Mean n people per sampling day	P
Sampling days ( <b>sdays</b> )	N days breeding site was sampled during breeding, per year	P
N toads ( <b>ntoads</b> )	Total n toads captured per year, including recaptures from the same year.	P

---

Rainfall data were obtained from the South African National Parks (SANParks) weather station at Silvermine (34.10°S, 18.44°E) and are in the form of monthly totals. Total annual rainfall (train) was used to test the effects of rainfall both prior to and post-breeding, on adult survival on recruitment rate. Total annual rainfall may also affect the recapture rate, as it may influence breeding activity regarding duration or intensity of breeding. Breeding season rainfall (brain) is the rainfall during the start of the breeding season only. Breeding rainfall may be important for: the formation of breeding aggregations, if adult toads respond to rainfall amount; the formation of the breeding puddles; the capacity and longevity of the breeding puddles – hence was used to test its effect on both recruitment and survival rates (which may be influenced by breeding behaviour). Development rainfall (drain) is rainfall during the larval development stages (eggs, tadpoles and metamorphs). Rainfall during this period is necessary to keep the puddles filled and the breeding site moist during development, and was thus only used to constrain recruitment parameters (not survival rate).

Drought-stress factors were calculated using a combination of daily temperature, humidity, wind speed and rainfall data from the Slangkop Weather Station (34.15°S, 18.33°E), and were obtained from TuTiempo.net. Vapour Pressure Deficit (VPD) was calculated using Tetens approximation formula (Tetens 1930). Evaporation rate  $E$  (mm) from a water surface was calculated per day using wind speed and outputs from the VPD calculation ( $e_a$  and  $e_s$ ), as calculated by Xu & Singh (1998). Precipitation-less-evaporation (pp-e) was the difference between the daily rainfall and calculated evaporation, and is a measure of the net atmospheric moisture deposition, or relative environmental moisture dependent on climatic water inputs and deficits. This would affect both the water level in the breeding puddles, and the general availability of moisture in the environment.

Annual maximum VPD (vpdmax), is the month with the highest mean evaporative gradient in the year, and may negatively affect adults and recruits, as well as the ability of adults to breed. It was hence used to test the effects of extreme drought-stress on adult survival rate as well as on recruitment rate. Development VPD maximum (dvpdmax) is the maximum monthly mean VPD during larval development. A month with a very high VPD during this period may cause the breeding puddle to evaporate, may place drought-stress on early recruits, and may thus affect recruitment rate negatively.

The total pp-e (tpp-e) is a measure of the total moisture inputs and deficits from the atmosphere during the year, and was used to test the overall effect of drought stress on both survival and recruitment rates. Breeding season pp-e (bpp-e), or mean pp-e during the start of breeding, is very similar to breeding rainfall, and was used to test the effect of over environmental moisture during the start of the breeding event (which may affect both adult behaviour at the breeding event and hence the breeding itself), on both survival and recruitment rate. Minimum annual pp-e (bpp-emin) is a measure of

the driest month in the year, or the month with the lowest monthly mean pp-e in the year. This was also used to test the effect of extreme drought-stress on adult survival rate and on juvenile survival, hence recruitment rate. Finally, minimum development pp-e (dpp-emin) is the month with the lowest net environmental moisture (from the atmosphere) during larval development. A month with a very low pp-e may cause the breeding puddles to dry up, and may result in the death of the tadpoles or eggs. Hence, dpp-emin was used to test the effect of extreme moisture unavailability during the development period on recruitment rate.

Sampling days (sdays) and N people per sampling day (ppsd) were used as measures of capture effort. However, because of the extreme variability of the number of toads at the breeding site, depending on the date relative to the breeding peak, sampling days and N people per sampling day were most likely poor measures of effort. Hence, N toads sampled (ntoads) was also used as a measure of capture effort and consisted of the total number of toads captured in a particular year, including recaptures of animals from that particular year (that were captured on a previous sampling day, but during the same sampling occasion/sampling year). Since only one recapture per individual per year was used in the CMR analysis, I deemed this measure of abundance to be sufficiently independent of the CMR data to be used as a covariate. These measures of capture effort, as well as some of the environmental covariates which may affect the breeding aggregation, were fitted to recapture rate (P) to test the possible influence of these factors on the estimated survival, seniority and recruitment rates (Table 2). These data were from recorded observations in the field notebooks, where the CMR data was also extracted from.

To find standardised abundance of toads at the breeding site (standardised to capture effort), which was used in correlative graphs, N toads was divided by N people sampling per sampling days. Another variable later used was the period of days that toads were

observed in the breeding puddles, which was also obtained from the field notebooks. Because the CMR-method was not a priority during the earlier years of the study, these data were not always recorded, and sampling occasions (within a year) were fewer and less standardised. Hence, this data from years 2007 and 2008 were removed from the two correlation graphs (Figs. 13 & 14). Program R (R Core Team 2013) was used for all regression analyses.

## RESULTS

During the course of the study period, from the total of 1600 animals that were sampled from the Silvermine site.

### **1. Survival models (and related results)**

For the survival models (Table 3), clearly the most parsimonious model was  $\phi(\text{brain}) P(t)$  – that is, survival rate constrained by breeding season rainfall and recapture rate fully time-dependent – which had more than 7 times more support from the data than the next AIC-best model, the fully time-dependent model  $\phi(t) P(t)$  (ratio of Akaike weights:  $= 0.787/0.091$ ). The  $\phi(t) P(t)$  model was only slightly better supported than the third best model,  $\phi(\text{train})P(t)$ , with survival constrained by total annual rainfall (ratio of Akaike weights:  $0.0913/0.0911$ ). The fourth AIC-best model was  $\phi(t) P(\text{brain})$ , which was considerably less well-supported by the data (Akaike weight: 0.025) than the previous three models (models 1, 2 & 3, Table 3). Hence, the effects of breeding season rain on recapture rate were not deemed important.

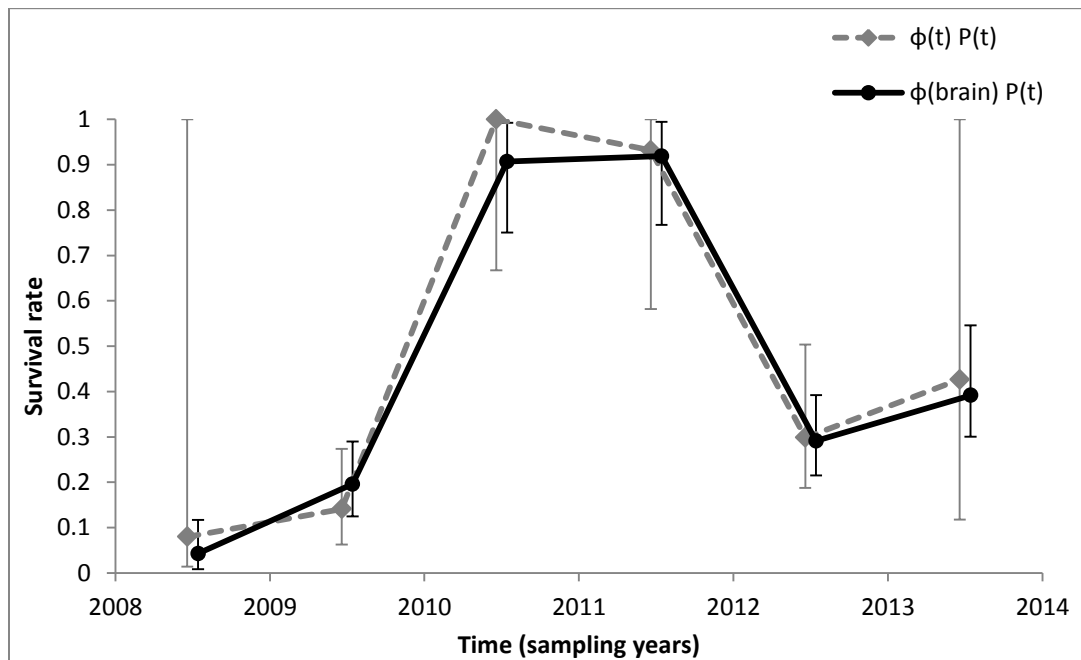
None of the drought-stress covariate (survival) were well-supported by the data (models 10, 14 & 15, Table 3), hence their effect on survival rate was deemed unimportant.

None of the capture effort covariate models were very parsimonious either (models 7, 8 and 9, Table 3), hence the effect of capture effort on recapture rate was not deemed important. Furthermore, none of the recapture rate covariate models were well-supported by the data.

**Table 3.** Model selection analysis of capture-mark-recapture models to estimate survival rate ( $\phi$ ) and recapture rate ( $P$ ), for Rose's mountain toadlet at Silvermine, South Africa. AICc denotes Akaike's Information Criterion, where lower values indicate better model fit;  $\Delta$  AICc notates the difference in AICc between the current model and the best model; Akaike weights ( $w$ ) is a measure of the relative support that the current model has from the data, compared to the other models; Num. Par is the number of parameters estimated in the current model; Deviance (Dev) is the difference in  $-2 \log$  Likelihood between the current model and the saturated model, or a model with the number of parameters equal to the sample size (Altwegg et al. 2003). Model notation for the Survival Models:  $\phi$ (survival constraint) $P$ (recapture constraint). See table 2 for an explanation of the covariates used; t denotes full time dependence.

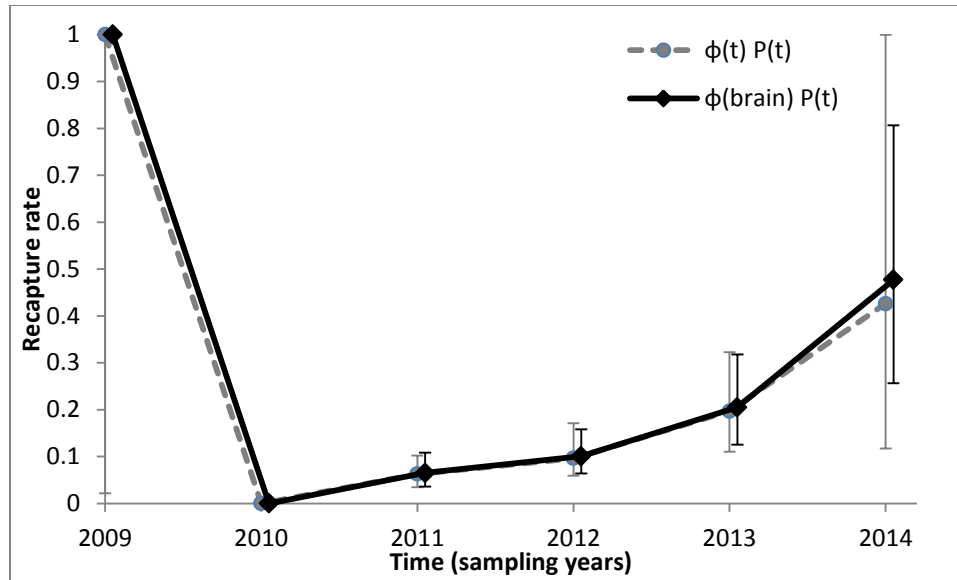
Model	AICc	$\Delta$ AICc	w	Num. Par	Dev
1. $\phi$ (brain) $P$ (t)	853.819	0	0.78716	8	18.7911
2. $\phi$ (t) $P$ (t)	858.1283	4.3093	0.09127	11	16.9695
3. $\phi$ (train) $P$ (t)	858.1326	4.3136	0.09107	8	23.1047
4. $\phi$ (t) $P$ (brain)	860.7064	6.8874	0.02515	8	25.6785
5. $\phi$ (tpp-e) $P$ (t)	866.1722	12.3532	0.00164	8	31.1443
6. $\phi$ (t) $P$ (sdays)	866.3837	12.5647	0.00147	8	31.3558
7. $\phi$ (t) $P$ (ntoads)	866.5226	12.7036	0.00137	8	31.4947
8. $\phi$ (t) $P$ (ppsd)	867.8921	14.0731	0.00069	8	32.8642
9. $\phi$ (pp-emin) $P$ (t)	870.6102	16.7912	0.00018	8	35.5823
10. $\phi$ (brain) $P$ (brain)	881.3952	27.5762	0	4	54.4801
11. $\phi$ (.) $P$ (t)	881.7747	27.9557	0	7	48.7816
12. $\phi$ (bpp-e) $P$ (t)	882.7395	28.9205	0	8	47.7116
13. $\phi$ (vpdmax) $P$ (t)	883.7684	29.9494	0	8	48.7405
14. $\phi$ (brain) $P$ (sdays)	889.5744	35.7554	0	4	62.6593

The two AIC-best models,  $\phi(\text{brain}) P(t)$  and  $\phi(t) P(t)$ , show that survival rate fluctuated drastically through time, with a bi-annual fluctuation pattern evident during the sampling period (Fig. 8). No gradual increasing or decreasing trend in survival rate over time was observed, although a gradually increasing trend in recapture rate over time was generally observed (Fig. 9).



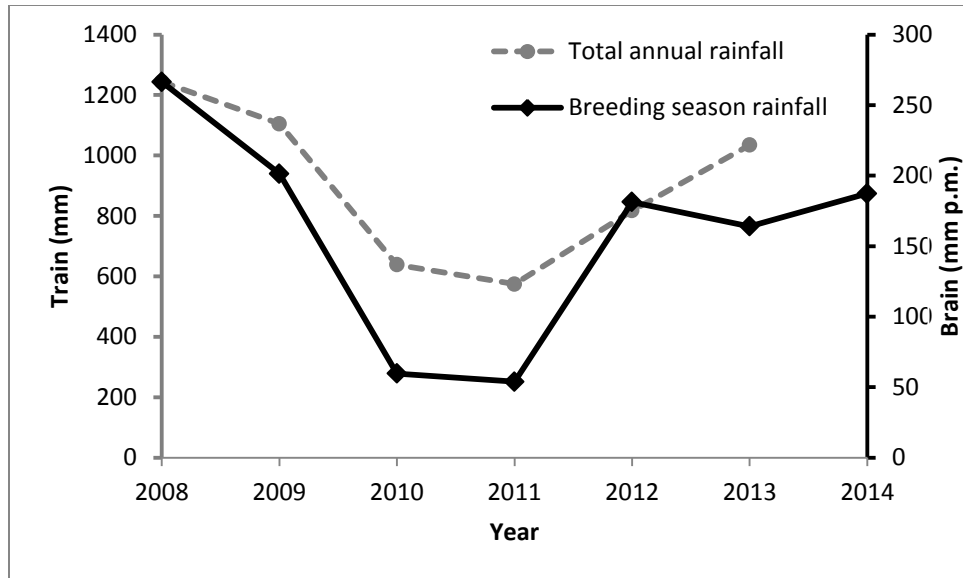
**Figure 8:** Survival rates over time from the basal model,  $\phi(\text{brain}) P(t)$  (blue dashed), and the AIC-best model,  $\phi(\text{brain}) P(t)$  (red solid). Model  $\phi(t) P(t)$  is fully time-dependent, while model  $\phi(\text{brain}) P(t)$  has survival rate constrained by breeding season rainfall. Probability (or rate) is on the Y axis; time in years on the X-axis, and each parameter is estimated for the period between two sampling years (i.e. the first graph point represents the survival rate for the period between 2008 and 2009, for both models). The bars indicate the 95% confidence intervals.



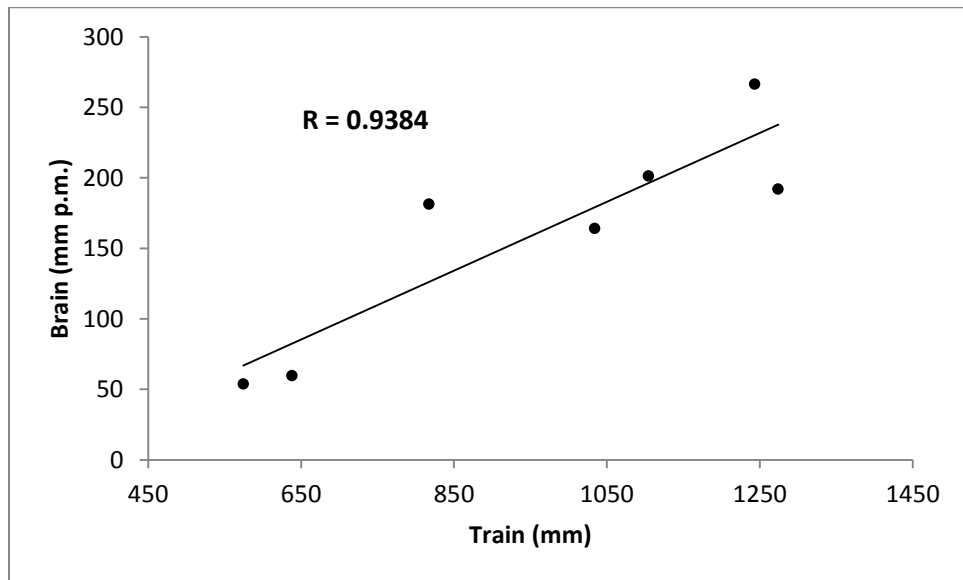


**Figure 9:** Recapture rates from the same models as in (Fig. 8) -  $\phi(t) P(t)$  basal, time-dependent model, and the AIC-best model  $\phi(\text{brain}) P(t)$ , in which survival rate was constrained by breeding season rain. Recapture rate is denoted on the Y axis; time in sampling years on the X-axis, and each parameter is estimated for the  $t_{i+1}$  year between two sampling years, or the year of *recapture* (i.e. between 2008 and 2009, the rate of 2008 animals being recaptured in 2009 is indicated). The bars indicate the 95% confidence intervals.

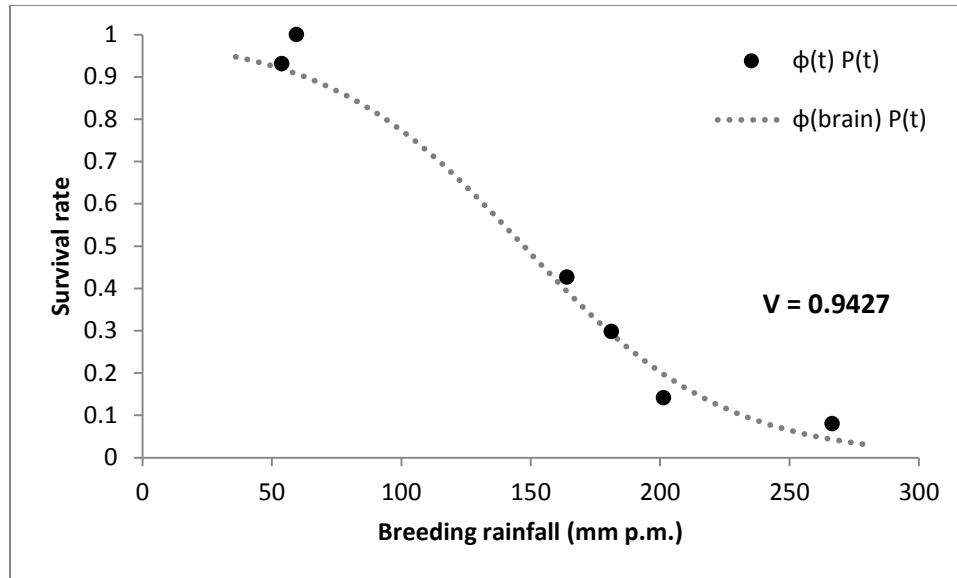
Rainfall during the breeding period had the most important effect on survival rate, from all covariate models tested (model 1, Table 3). Although breeding season rainfall and total annual rainfall followed a similar pattern over time (Fig. 10), and were significantly positively correlated ( $R = 0.94$ ,  $t = 5.4319$ ,  $df = 4$ ,  $p = 0.0056$ , Fig. 11), the model  $\phi(\text{brain}) P(t)$  was more than eight times better supported by the data than the  $\phi(\text{train}) P(t)$  model (ratio of Aikake weights:  $0.787/0.091$ , Table 3). I found a highly significant negative relationship between survival rate and mean monthly rainfall during the breeding period (Fig. 12), as breeding rainfall explained 94% of the variability in survival rate over time.



**Figure 10:** This shows the trend in (model covariates) total annual rainfall and breeding season rainfall over the sampling period. Total annual rainfall (grey dashed) is denoted on the Y-axis on the left. Breeding season rainfall (black solid), or the mean monthly rainfall during the start of breeding (Jul-Aug), is denoted on the Y-axis on the right. The last value for total annual rainfall was not available yet (because data were gathered in September 2014).

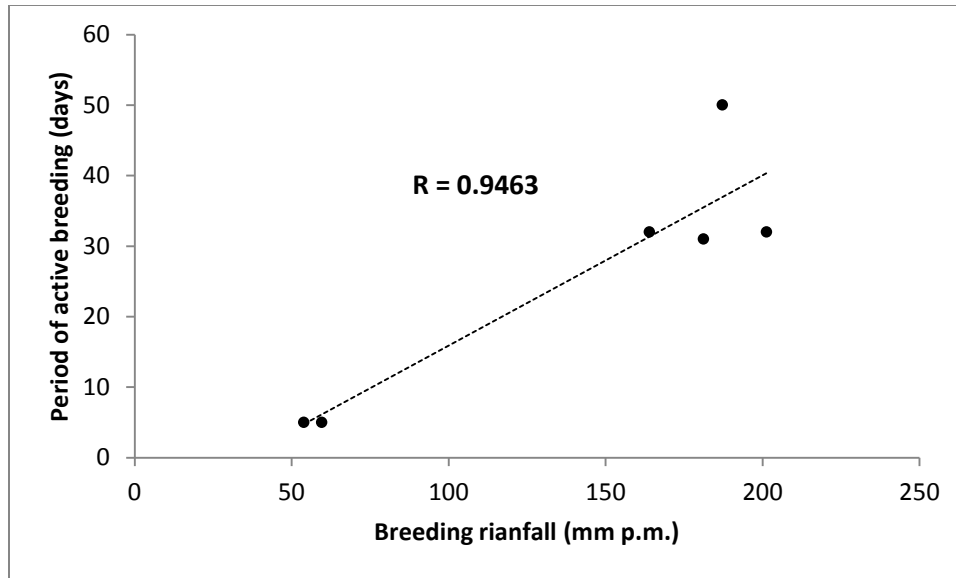


**Figure 11:** This shows the positive relationship between model covariates breeding season rainfall (mean monthly rainfall during the start of breeding, Jul-Aug) and total annual rainfall (mm per year). The linear regression fitted was highly significant ( $t = 5.4319$ ,  $df = 4$ ,  $p = 0.005573$ ).

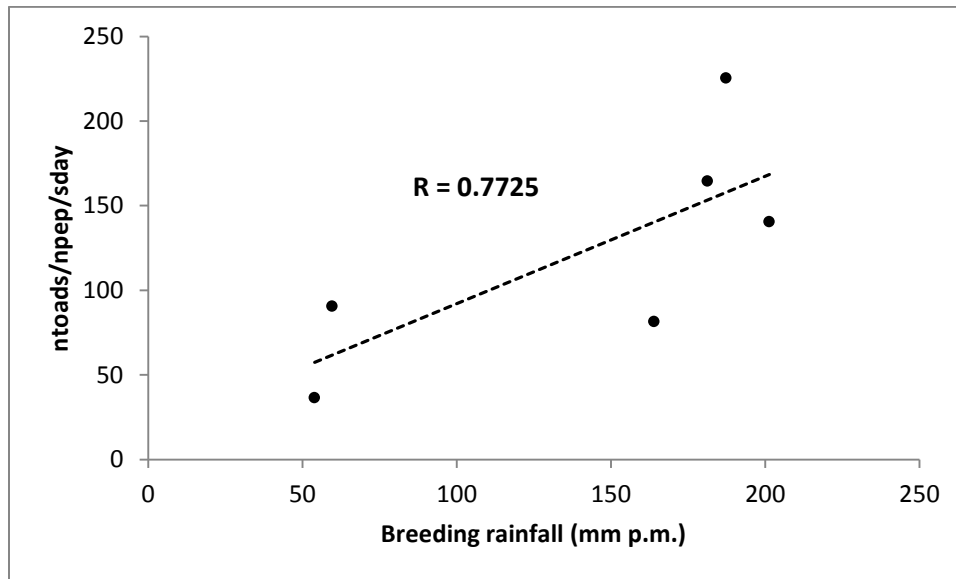


**Figure 12:** The estimated survival rates (as in Fig. 8) from the fully time-dependant model  $\phi(t) P(t)$  are presented as data points per sampling year. The predicted survival rates for a continuous range of breeding rainfall values, from the AIC-best model,  $\phi(\text{brain}) P(t)$  (in which survival rate was constrained by breeding season rainfall), are presented as a dotted grey line. Both estimates are plotted over breeding season rainfall (mean monthly rainfall during the start of breeding in mm). Note the strong negative trend and close fit of the fully time-dependent model estimates on the predicted values from the (breeding season rainfall) covariate model. Survival rates are GLM outputs, hence no correlation coefficient is given. Analysis of deviance shows that 94% of the variability in survival rate over time is explained by breeding rainfall.

The period that toads remained active at the breeding site was positively and significantly correlated to breeding season rainfall ( $R = 0.95$ ,  $t = 5.069$ ,  $df = 3$ ,  $p = 0.015$ , Fig. 13), thus indicating a longer active breeding period during years of higher breeding season rainfall. Furthermore, the standardised abundance of toads at the breeding site also showed a positive relationship with breeding season rainfall (Fig. 14), although the linear regression fitted was non-significant ( $R = 0.77$ ,  $t = 2.11$ ,  $df = 3$ ,  $p = 0.126$ , Fig. 14).



**Figure 13:** This shows the positive relationship between the breeding period (period between first and last observed adult activity at the breeding puddles) and the mean monthly rainfall during the start of breeding. Years 2007 and 2008 were excluded due to data uncertainties and lack of sampling effort. The linear regression fitted (dotted line) was highly significant ( $t = 5.0685$ ,  $df = 3$ ,  $p = 0.0148$ ).



**Figure 14:** Standardised abundance at breeding site (n toads sampled per n people sampling per n sampling days) over breeding season rainfall (mean monthly rainfall during the start of the breeding period, July-Aug). Years 2007 and 2008 were excluded due to data uncertainties and lack of sampling effort. The linear regression fitted was not significant ( $t = 2.1071$ ,  $df = 3$ ,  $p = 0.1257$ ).

## 2. Seniority models

The AIC-best model  $\gamma(\text{train}) P(t)$ , where seniority rate was constrained to be a function of total annual rainfall, was only slightly better supported by the data than the next AIC-best model  $\gamma(t)P(\text{sdays})$ , with recapture rate constrained by N sampling days (ratio of Akaike weights: 0.288/0.285, Table 4). The model  $\gamma(\text{brain}) P(\text{sdays})$ , however, was not well-supported by the data (Akaike weight: 0.0, model 15, Table 4). The positive relationship found between total annual rainfall and inverse seniority rate (or proportion of new recruits) was significant, as total annual rainfall explained 84.3% of the total variability in seniority rate over time.

The third AIC-best model was  $\gamma(\text{pp-emin}) P(t)$  (Akaike weight 0.151, Table 4), and shows that drought-stress in the driest month of the year may also have an important effect on recruitment, as it explained 80% of the variability in seniority rate over time ( $V = 0.8008$ ). The AIC-best model  $\gamma(\text{train}) P(t)$  was approximately twice as well-supported by the data as the basal, fully time-dependent model  $\gamma(t) P(t)$  (ratio of Akaike weights: 0.29/0.15, models 1 & 4, Table 4).

**Table 4:** Model selection analysis of capture-mark-recapture models to estimate seniority rate( $\gamma$ ) and recapture rate (P) for Rose's mountain toad at Silvermine, South Africa. AICc denotes Akaike's Information Criterion, where lower values indicate better model fit;  $\Delta$  AICc notates the difference in AICc between the current model and the best model; Akaike weights (w) is a measure of the relative support that the current model has from the data, compared to the other models; Num. Par is the number of parameters estimated in the current model; Deviance (Dev), is the  $-2 \log$  Likelihood of the current model. Model notation for the seniority models :  $\gamma$ (seniority rate constraint) P(recapture rate constraint). See table 2 for an explanation of the covariates used; t denotes full time dependence.

Model	AICc	$\Delta$ AICc	w	Num. Par	Dev
1. $\gamma$ (train)P(t)	955.9444	0	0.28835	8	939.8471
2. $\gamma$ (t)P(sdays)	955.9707	0.0263	0.28459	8	939.8734
3. $\gamma$ (pp-e)P(t)	957.2426	1.2982	0.15067	8	941.1454
4. $\gamma$ (t)P(t)	957.2595	1.3151	0.1494	11	935.0809
5. $\gamma$ (bpp-e)P(t)	959.0722	3.1278	0.06036	8	942.975
6. $\gamma$ (tpp-e)P(t)	959.7103	3.7659	0.04387	8	943.6131
7. $\gamma$ (dvpdmax)P(t)	961.9943	6.0499	0.014	8	945.897
8. $\gamma$ (t)P(nfrogs)	964.0269	8.0825	0.00507	8	947.9297
9. $\gamma$ (t)P(ppsd)	964.9261	8.9817	0.00323	8	948.8289
10. $\gamma$ (dpp-e)P(t)	969.7295	13.7851	0.00029	8	953.6323
11. $\gamma$ (vpdmax)P(t)	970.9425	14.9981	0.00016	8	954.8453
12. $\gamma$ (drain)P(t)	977.9628	22.0184	0	8	961.8656
13. $\gamma$ (.)P(t)	979.5942	23.6498	0	7	965.5186
14. $\gamma$ (brain)P(t)	979.6537	23.7093	0	8	963.5564
15. $\gamma$ (train)P(sdays)	981.5211	25.5767	0	4	973.4941

### 3. Combined survival and recruitment models

The best combined Pradel model  $\phi$ (brain) P(t) F(t), with survival rate constrained as a function of breeding season rainfall, was only slightly better supported by the data than the next AIC-best model  $\phi$ (t) P(t) F(train), with recruitment rate constrained as a function of total annual rainfall (ratio of Akaike weights: 0.219/0.218). Thus rainfall was found to be the most important factor affecting both survival and recruitment rate. However, drought-stress during the driest month of the year, annual minimum pp-e,

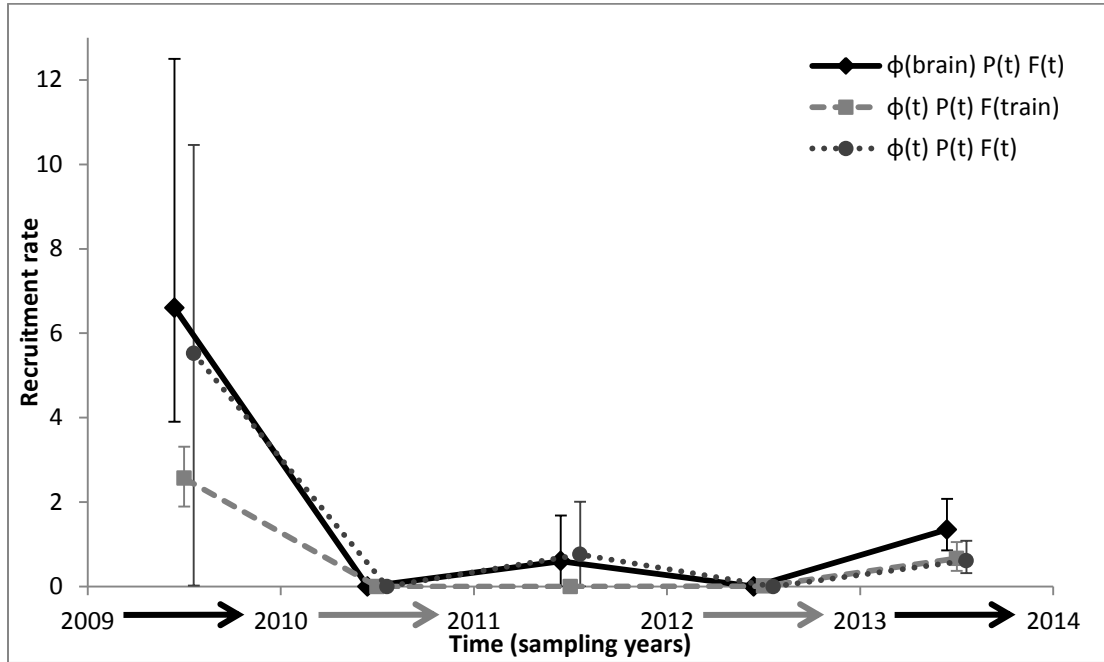
was also an important covariate of recruitment rate, and was better supported by the data than the basal model  $\phi(t) P(t) F(t)$  (models 4 & 5, Table 5; ratio of Akaike weights: 0.16/0.13). There was no clear AIC-best model among the top 5 models, with the AIC-best model being less than twice as well-supported by the data as the fifth AIC-best model (ratio of Akaike weights: 0.22/0.13; models 1 & 5, Table 5).

**Table 5:** Model selection analysis of capture-mark-recapture models to estimate survival rate ( $\phi$ ), recapture rate ( $P$ ) and recruitment rate ( $F$ ), for Rose's mountain toadlet at Silvermine, South Africa. AICc denotes Akaike's Information Criterion, where lower values indicate better model fit;  $\Delta$  AICc notates the difference in AICc between the current model and the best model; Akaike weight ( $w$ ) is a measure of the relative support that the current model has from the data, compared to the other models; Num. Par is the number of parameters estimated in the current model; Deviance (Dev), is the  $-2$  log Likelihood of the current model. Model notation for the survival and recruitment models:  $\phi$ (survival rate constraint)  $P$ (recapture rate constraint)  $F$ (recruitment rate constraint). See table 2 for an explanation of the covariates used;  $t$  denotes full time dependence.

Model	AICc	$\Delta$ AICc	w	Num. Par	Dev
1. $\phi(\text{brain})P(t)F(t)$	5379.061	0	0.21917	15	5348.736
2. $\phi(t)P(t)F(\text{train})$	5379.076	0.0142	0.21762	15	5348.75
3. $\phi(\text{train})P(t)F(t)$	5379.443	0.3814	0.18112	15	5349.117
4. $\phi(t)P(t)F(\text{pp-emin})$	5379.651	0.5896	0.16321	15	5349.325
5. $\phi(t)P(t)F(t)$	5380.086	1.0245	0.13131	17	5345.67
6. $\phi(t)P(t)F(.)$	5382.189	3.1276	0.04588	11	5360.01
7. $\phi(t)P(t)F(\text{bpp-e})$	5382.444	3.3823	0.04039	15	5352.118
8. $\phi(t)P(\text{sdays})F(t)$	5390.369	11.308	0.00077	15	5360.044
9. $\phi(\text{brain})P(t)F(\text{train})$	5391.095	12.0332	0.00053	13	5364.848

The recruitment rates from the two most parsimonious combined models and the basal model (models 1, 2 and 5, Table 5), although different, show the same basic fluctuations over time. The recruitment rate is highly unstable over time (Fig. 15). The recruitment rate for the period 2009-2010 is very high (between  $\sim 2.2$ -6.2), but drops rapidly thereafter, and remains below 2.0 until 2014 (Fig. 15). All three the models displayed

(Fig. 15) show a recruitment failure, or very low recruitment rate, for the periods 2010-2011 and 2012-2013 respectively.



**Figure 15:** Recruitment rates from the three AIC-best models (Table 5):  $\phi(\text{brain}) P(t) F(t)$ , with survival constrained as a function of breeding season rain;  $\phi(t) P(t) F(\text{train})$ , with recruitment rate constrained by total annual rainfall;  $\phi(t) P(t) F(t)$ , with all parameters fully time dependent, over time. Recruitment rate is the number of new recruits in the population in year  $t_{i+1}$  (i.e. 2010 for the first data point), per animal in the population in year  $t_i$  (i.e. 2009 for the first data point), and is denoted on the Y-axis. Time in sampling years is on the X-axis, with each recruitment estimate given for the period between two successive sampling years (i.e. the first data point is for the period 2009-2010). The black arrows indicate relatively high recruitment rates between two years (among the three models), while the grey arrows indicate virtually no recruitment between two years. Error bars indicate 95% confidence intervals.

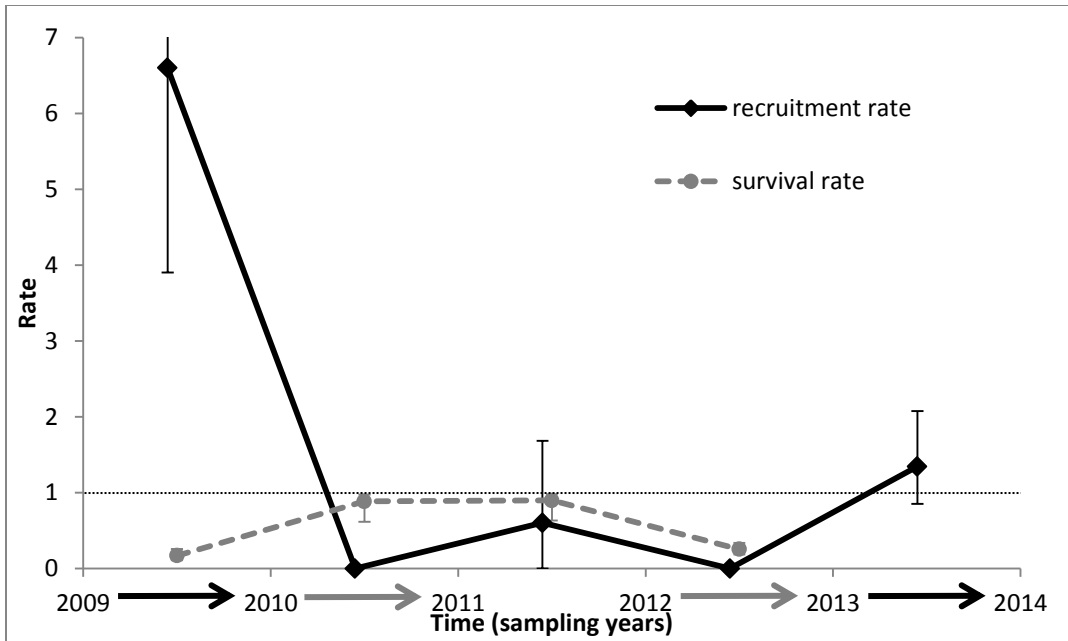
According to the most parsimonious model  $\phi(\text{brain}) P(t) F(t)$  (Fig. 16), the period of highest recruitment, 2009-2010, was accompanied by a very low survival rate.



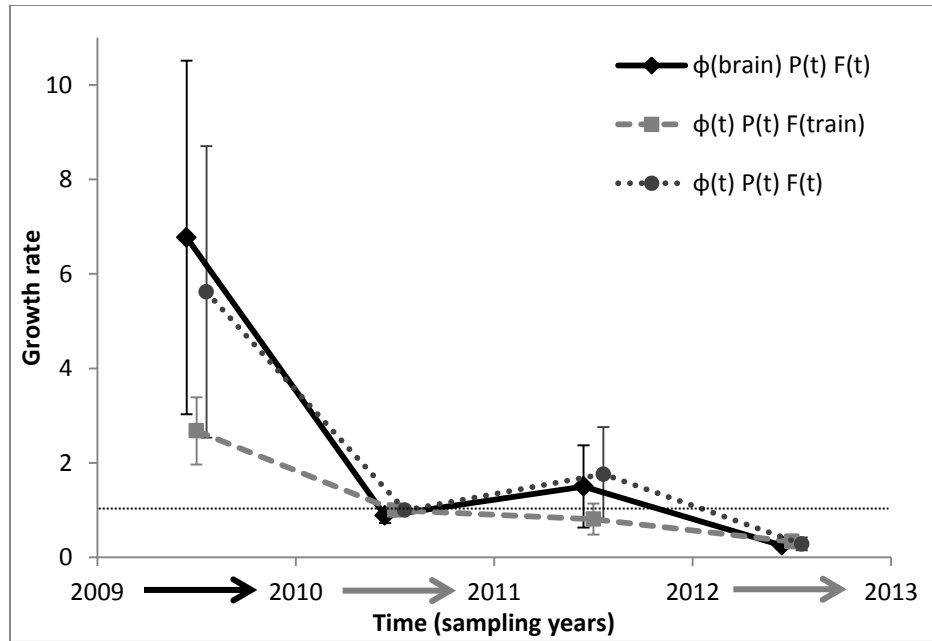
Thereafter, recruitment rate remains below 1.0, except during the period 2013-2014 (Fig. 16). The period 2010-2011 shows the opposite, with a very high survival rate and a very low recruitment rate. However, this oppositely fluctuating pattern does not continue for the periods 2011-2012, or 2012-2013, which has a low recruitment and survival rate (Fig. 16).

The derived estimates of population growth rate from the two AIC-best models and the basal model (Fig. 17) all show the same decreasing trend in population growth over time. The high growth rate for 2009-2010 (Fig. 17) is due to the high recruitment rate, and despite the low survival rate during this period (Fig. 16). The population is stable during 2010-2011 (Fig. 17), due to high survival rates and despite virtually no recruitment during this period (Fig. 16). The population then grows (2011-2012, Fig. 17) due to high survival and moderate recruitment rates (Fig. 16), and declines thereafter due to low survival and recruitment rates during 2012-2013 (Figs. 16 & 17).

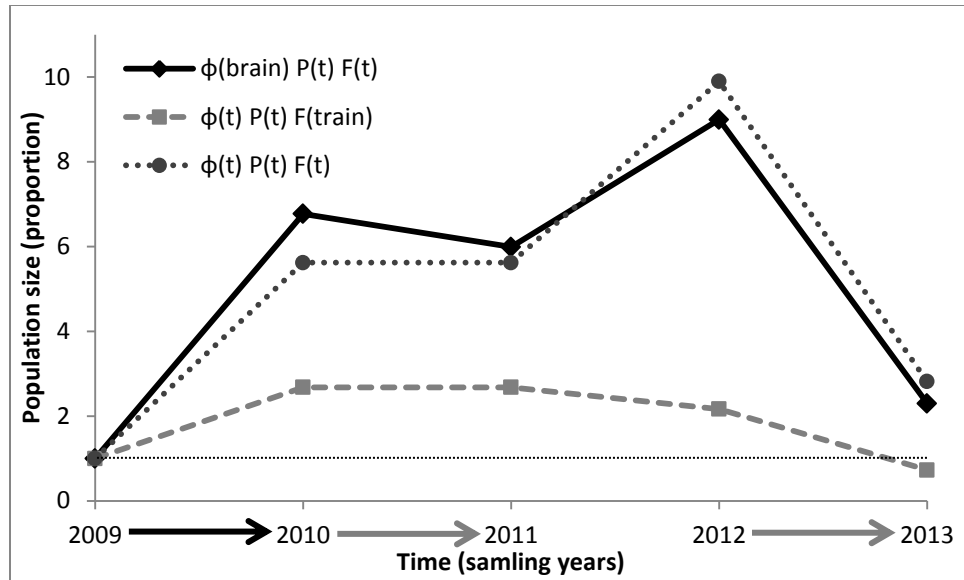
According to the derived growth rate estimates from the most parsimonious model  $\phi(t) P(t) F(t)$ , as well as the basal time-dependent model, the population size (Fig. 18) fluctuates considerably during the course of the study. However, according to the second AIC-best model,  $\phi(\text{train}) P(t) F(t)$ , the population size shows more gradually changing trend over time (Fig. 18). Overall, the models suggest an increasing trend in population size from 2009 to a peak size in 2012, followed by relatively rapid decline in 2013 (Fig. 18). Although I was unable to estimate the growth rate or population size for 2008 and 2014, there is very evidence in the models to suggest an overall decline in population size during the study period, while there is some evidence for an increase in population size (Fig. 18; last recruitment value, Fig. 16).



**Figure 16:** Survival rate (grey dashed) and recruitment rate (black solid) from the AIC-best model  $\phi(\text{brain}) P(t) F(t)$  (Table 5), in which survival rate was constrained to vary as a function of breeding season rainfall, over time. Rate is on the Y axis, time in sampling years is on the X-axis. Survival rate cannot exceed 1.0, as it is the proportion of individuals from occasion  $t_i$  (i.e. 2009 for the first data point) that survived to  $t_{i+1}$  (i.e. 2010 for the first data point). However, recruitment rate is the number of newly recruited animals in the population at occasion  $t_{i+1}$ , per animal present in the population at  $t_i$ , and can thus exceed 1. Estimates are shown for the period between two successive sampling years (e.g. 2009-2010 for the first data point). The bars indicate 95% confidence intervals for each estimate. The black arrows indicate recruitment rates  $>1$  between two sampling years, while grey arrows indicate very low recruitment ( $F \sim 0.0$ ). The last survival parameter was not estimable, and was excluded from the graph.



**Figure 17:** Derived estimates of population growth rates from the three AIC-best combined Pradel models (Table 5):  $\phi(\text{brain}) P(t) F(t)$ , with survival constrained by breeding season rain;  $\phi(t) P(t) F(\text{train})$ , with recruitment rate constrained by total annual rainfall;  $\phi(t) P(t) F(t)$ , with all parameters fully time dependent. Growth rate is the proportional size difference in the population from one sampling year to the next (hence growth rate  $>1$  shows positive growth,  $<1$  shows negative growth,  $=1$  shows no growth), and is denoted on the Y-axis. Time in sampling years is on the X-axis, with each growth estimate given for the period between two successive sampling years, or from one sampling year to the next (i.e. the first data point for each model is for the period 2009-2010). The black arrows indicate relatively high recruitment rates between two years, while the grey arrows indicate virtually no recruitment ( $F \sim 0$ ) between two years. Error bars indicate 95% confidence intervals.



**Figure 18:** Predicted relative population size over time, calculated from the derived growth rates (Fig. 15) from the three AIC-best combined Pradel models (Table 5). The population size, denoted on the Y-axis, is relative to the “original” population in the first year after which recruitment rate could be estimated, 2009 (population size=1). These values are not model estimates (but simply indicate the trends from Fig. 15 in terms of population size, rather than growth), hence no confidence intervals are shown.

## DISCUSSION

The main aim of the study was to find the first estimates of survival and recruitment rates for *Capensibufo rosei*, which I have done. I then aimed to identify the main trends in population demographics over time, and to relate these trends to environmental variables in order to identify possible environmental drivers of these trends.

Firstly I hypothesised that the demographic parameters are likely to be unstable over time, if the population is small and range-restricted (hypothesis 1). As expected, the survival models show an unstable survival rate which fluctuates drastically through the relatively short, 7-year study period (Fig. 8). The Pradel models suggest an equally unstable pattern of recruitment rate over time (Figs. 15 & 16). The population growth rate (Fig. 17) does not fluctuate as much, but shows a generally decreasing trend over time. The population size (Fig. 18) was also unstable, showing some fluctuation, mostly positive, during the study period, due to the fluctuating survival and recruitment rates. Such unstable demographic parameters suggest a small population size and range, with population parameters which may be strongly influenced by changing local environmental factors.

Secondly, I expected survival rate to relate positively to rainfall, but negatively to drought-stress (hypothesis 2). Although none of the drought-stress covariates showed a strong relationship with survival rate over time (models 5, 9, 12 and 13, Table 3), rainfall during the start of the breeding period (breeding season rainfall) explained 94% of the variability in survival rate over time (model 1, Table 3). However, completely contrary to expectations, this highly significant relationship between breeding season rainfall and survival rate was negative (Fig. 12). This does not suggest that rainfall during breeding causes high adult mortality at the breeding puddles. Breeding rainfall is calculated for the months of July and August, while the bulk of the toads were only sampled in August, and some still in September (Fig. 2), and survival is calculated for the period after initial

capture to the next sampling year. Rather, I suggest that rainfall during this period may affect the formation or duration of the breeding aggregations, in a way that affects adult survival thereafter.

Being an explosive breeder, hundreds of *Capensibufo rosei* adults gather densely in the few small breeding puddles during the breeding season. Intra-sexual competition between males is intensive in these aggregations, and may be highly energetically costly. Although high cost of breeding is generally associated with females, studies on other explosive breeding toads have also shown a significant energetic cost on males during breeding, as a result of courtship behaviour. These studies generally found high energetic costs associated with male calling (Woolbright 1983; Fairchild 1984). However, *C. rosei* males do not call and females do not approach individual calling males, as is the case with most other toads. Rather, *C. rosei* males rely entirely on moving around in and between breeding puddles to find females before the other males do. This results in a lot of physical movement and brawling among males, for possession of a female, and balls of frenzied males have often been observed around a single female, even drowning the female on occasion. Furthermore, the proportion of recaptured males during a particular sampling year, generally increased per sampling occasion, and is evidence that males remain at the breeding puddles for much of the breeding period. Thus, breeding males may have less or no time to forage during breeding. Reduced food intake, combined with the extra energy expense of breeding and intra-sexual competition, may greatly reduce stored energy in the body, hence weakening it. By simple observations, the males after and at the end of breeding often appear very skinny, compared to those before and during the early stages of breeding. Although I did not quantify the physiological cost of breeding on male toads directly, the drastic drop in survival rates after years of high breeding season rainfall may well be explained by an increase of highly costly breeding activity during years of higher breeding season

rainfall. As most of the adults sampled were males (~92% of toads sampled during the study period), the observed trends in survival were dominated by male-data.

If the cost of breeding can cause the observed fluctuations in survival rate over time, then breeding activity between years must vary, and must be positively related to breeding season rainfall. My results show that the period of active breeding increases with increasing breeding season rainfall (Fig. 13), during the years for which this data were available. Such an extension of the active breeding period during years of higher breeding season rainfall would incur a greater cost on breeding males, for a prolonged period of time.

Furthermore, the generally low recapture rates (Fig. 13) despite relatively high survival rates for some years (Fig. 12), may suggest that not all animals return to breed every year. Individuals captured in one sampling year, and subsequently recaptured two or more years later, were a common occurrence in the raw CMR data. This could be due to low detectability. However, the varying numbers of toads sampled over the years, and the generally observed varying number of toads present at the breeding site in different years, may also indicate varying intensities of breeding activity between years. Although not significant due to a lack of recorded data and a standardised method of quantifying toad abundance, my data shows a positive relationship between the number of toads sampled per person per sampling day, and breeding season rainfall (Fig. 14).

Varying abundance of adult males at a breeding site is a commonly observed trait among other explosive breeding toads, although generally observed between breeding bouts in a particular year (Wagner et al. 1992; Wells 1979). However, since these toads only breed once a year, this pattern may be translated into an inter-annual pattern. If the amount of toads that arrive to breed varies positively with breeding rainfall as suggested, the amount of adults exposed to the cost of breeding would be higher in years of higher breeding season rainfall, contributing to the variation in observed

survival rate over time. Furthermore, increased male abundance at the breeding site may also influence intra-sexual competition dynamics, hence changing the cost associated with breeding (Fairchild 1984).

According to hypothesis 3, I expected that recruitment rate would relate positively to rainfall, but negatively to drought-stress. There was no clear AIC-best model among the seniority models (Table 4), or among the combined survival and recruitment models (Table 5). This may be because recruitment can be affected by a complex range of interacting factors, which can vary in their effect on recruits at different life-stages. Although breeding season rainfall was not important covariate of seniority rate (model 14, Table 4), the total annual rainfall (model 1, Table 4) explained 84% of the variability in seniority rate over time (seniority rate being an inverse measure of recruitment). For a better understanding of factors which influence recruitment, more information on the different life-history stages is required for the species.

Drought-stress, in terms of the driest month of the year, or minimum annual pp-e, showed a negative relationship with recruitment rate as expected (model 4, Table 5), explaining 74.5% of the variability in recruitment rate over time. However, the two most parsimonious combined survival and recruitment models,  $\phi(\text{brain}) P(t) F(t)$  and  $\phi(t) P(t) F(\text{train})$  respectively (ratio of Akaike weights: 0.219/0.218, Table 5), showed that rainfall was the most important determining factor for both survival and recruitment rate. Annual minimum pp-e was also partially calculated from rainfall, and supports this finding.

Lastly, I hypothesised that recruitment rate, rather than survival rate, would be the more important contributing factor to population growth rate and size, indicating that the species is relatively R-selected (hypothesis 4). This pattern was not clearly distinguishable from the models, as both recruitment and survival rates fluctuated between very high (survival rate  $\sim 1.0$ , Fig. 8; recruitment rate  $\sim 6.5$ , Fig. 16) and very low



(survival and recruitment rate  $\sim 0.0$ , Fig.s 8 & 16), with recruitment rate only exceeding 1 (recruit produced per adult in the population the previous year) for the periods 2009-2010 and 2013-2014 (Fig. 16).

However, the high recruitment during 2009-2010 (Fig.s 15 & 16) shows that recruitment rate can be very high during years of high breeding rainfall (Fig. 10), and can more than compensate for low adult survival rates, as indicated by the high growth rate despite the low survival rate for this period (2009-2010, Fig. 16). Furthermore, the models suggest that, while only high recruitment rates can cause high population growth rates, high survival rates during years of poor recruitment (Fig. 16) can keep the population stable (2010-2011, Fig. 17), or even increasing in size (2011-2012, Fig. 17). Hence, higher adult survival rates during years of lower breeding season rainfall, can buffer the population size (Fig. 18), despite low recruitment success during such years.

The fluctuation in survival rate observed is far more drastic and over a much shorter time-span than generally found in other CMR studies that used the same kind of models (Schmidt et al. 2002; Griffiths et al. 2010; Baker et al. 2004; Altwegg & Reyer 2003; Pike et al. 2008). My findings show evidence for extreme rainfall-induced life-history plasticity. Hence, it is probably not accurate to suggest that the species is R-selected, although the recruitment rate after good rainfall year can be very high, and adult survival rate can be very low. Rather, I suggest that variability in rainfall during and immediately prior to breeding, can stimulate a varied behavioural response from the adults in terms of breeding investment – either through the duration of the breeding period or the amount of adults which arrive to breed.

More concisely, I suggest that most adults maximise their investment in breeding when the conditions are optimal, but invest in survival during years when conditions are sub-optimal. This mechanism of population resilience may be an adaptation to the highly

variable microclimate of the mountainous regions in the Western Cape, and the temporal nature of the puddles on which their breeding success depends.

The number of toads sampled during 2014 (631) was the largest number sampled during the course of the study. Two new satellite breeding puddles were observed for the first time in 2014 during the course of the study period, one of which contained hundreds of toads and thousands of eggs during the breeding peak. This phenomenon may be an indication of population expansion. The models indicate a growing trend in population size (Fig. 18) from 2009 to 2012, with a drop in population size in 2013, although the recruitment rate for 2013-2014 was  $\sim 1.3$  (Fig. 16), possibly indicating an increase in population size between 2013 and 2014.

However, the instability of all population parameters including population size over the relatively short study period, suggests that the population may be relatively small, and may be at high risk of extinction due to stochastic events or catastrophes. Furthermore, because the breeding period appears critical not only in determining breeding success, but also adult survival, the breeding site may be the key pivot-point on which the population success is balanced. More precisely, because of the risky trade-off between survival and reproductive output shown by the data, a disturbance at the breeding site, particularly during a “good” breeding year, can have potentially catastrophic effects on the population size in a very short span of time. If disturbances at the breeding site happen in consecutive “good breeding” years, adult losses due to over-investment in a failed breeding attempt can potentially drive numbers below a certain threshold point, and lead to population collapse. Furthermore, because of the strong link between demographic parameters and rainfall, this species may be very sensitive to future climate change.

The accuracy of my models may have been negatively affected by false markings, such as natural loss of a toe, or by missing marks while processing. However, toe-clipping as a

form of marking has been shown to be the most effective method for correctly identifying recaptures in frogs, particularly over inter-annual periods (Rannelly et al. 2013). Furthermore, although no evidence currently suggests other breeding populations or any form of a metapopulation structure, I cannot completely rule out the possibility of migration, particularly permanent emigration of dispersing juveniles.

In conclusion, I identified a number of key research gaps for the species, as well as a list of recommendations regarding the conservation management of the species, based on the findings:

Research recommendations:

1. Controlled larval development experiments are needed to identify potential factors of importance to recruitment.
2. Toad weights before, during and after breeding are required to better quantify energetic costs of breeding.
3. A more standardised method for quantifying variation in adult abundance and activity at the breeding site, within and across breeding years, is needed to better understand the observed relationship between these variables and climate.
4. Identification of individuals (rather than just batch-marks) will provide very powerful data on dynamics at the breeding site, adult behaviour and movements, ageing individuals, and identifying possible migration patterns. I recommend testing dorsal markings as a method of individual identification. See also: (Gamble et al. 2007; Bradfield 2004). If this method is shown to be reliable, it may also be more viable in the long-term, may provide more reliable recapture histories not subject to natural losses of toes, and may be more ethically sound than toe-clipping.
5. Longer-term CMR monitoring is needed to better understand population trends in response to changing environmental and climatic variables.

### Management recommendations:

1. Conservation efforts should focus on keeping the breeding sites pristine. Current practices, such as cages over the breeding puddles to prevent disturbance from predators and people, closing the path during breeding, but keeping it open after the new recruits have left, seem to be effective in keeping the population relatively healthy.
2. Efforts to find possibly unknown breeding sites should continue, particularly close to the currently known breeding sites. If found, such populations may also shed light on migration and dispersal possibilities.
3. Identification and mapping of future potential breeding sites is needed, in case of a catastrophe or decline at the current breeding sites.
4. Transfer experiments of eggs to new potential breeding sites are needed to test the possibility of translocation in case of future declines or catastrophes.
5. The restoration (or re-introduction) of extinct historic breeding sites should be considered.

## REFERENCES

- Altwegg, R. et al., 2003. Variation and covariation in survival, dispersal, and population size in barn owls *Tyto alba*. *Journal of Animal Ecology*, 72(3), pp.391–399. Available at: <http://doi.wiley.com/10.1046/j.1365-2656.2003.00706.x>.
- Altwegg, R. & Reyer, H., 2003. Patterns of Natural Selection on Size at Metamorphosis in Water Frogs. *Evolution*, 57(4), pp.872–882.
- Anderson, A.D.R., Burnham, K.P. & White, G.C., 1994. AIC MODEL SELECTION IN OVERDISPERSED CAPTURE-RECAPTURE DATA. *Ecology*, 75(6), pp.1780–1793.
- Anderson, D.R. & Burnham, K.P., 2002. Avoiding Pitfalls When Using Information-Theoretic Methods. *The Journal of Wildlife Management*, 66(3), pp.912–918.
- Baker, A.J. et al., 2004. Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. *Proceedings. Biological sciences / The Royal Society*, 271(1541), pp.875–882. Available at: <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1691665&tool=pmcentrez&rendertype=abstract> [Accessed September 23, 2014].
- Baldwin, R.F., Calhoun, A.J.K. & DeMaynadier, P.G., 2006. Society for the Study of Amphibians and Reptiles Conservation Planning for Amphibian Species with Complex Habitat Requirements: A Case Study Using Movements and Habitat Selection of the Wood Frog *Rana sylvatica* Conservation Planning for Amphibian Species. *Journal of Herpetology*, 40(4), pp.442–453.
- Beebee, T.J.C., 2005. Conservation genetics of amphibians. *Heredity*, 95, pp.423–427.
- Bengtsson, J. et al., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. *Forest Ecology and Management*, 132, pp.39–50.
- Blanco, M.A. & Sherman, P.W., 2005. Maximum longevity of chemically protected and non-protected fishes, reptiles, and amphibians support evolutionary hypotheses of aging. *Mechanisms of ageing and development*, 126(6-7), pp.794–803. Available at: <http://www.ncbi.nlm.nih.gov/pubmed/15888334> [Accessed September 20, 2014].
- Blaustein, A.R., Belden, L.K., Olson, D.H., Green, D.M., Terry, L., et al., 2001. Amphibian Breeding and Climate Change. *Conservation Biology*, 15(6), pp.1804–1809.
- Blaustein, A.R., Belden, L.K., Olson, D.H., Green, D.M., Root, T.L., et al., 2001. Amphibian Breeding and Climate Change. *Conservation Biology*, 15(6), pp.1804–1809.
- Blaustein, A.R. & Kiesecker, J.M., 2002. Complexity in conservation: lessons from the global decline of amphibian populations. *Ecology Letters*, 5(4), pp.597–608. Available at: <http://doi.wiley.com/10.1046/j.1461-0248.2002.00352.x>.

- Blaustein, A.R., Wake, D.B. & Sousa, W.P., 1994. Amphibian Declines: Judging Stability , Persistence , and Susceptibility of Populations to Local and Global Extinctions. *Conservation Biology*, 8(1), pp.60–71.
- Bradfield, K.S., 2004. Photographic identification of individual Archey 's frogs , *Leiopelma archeyi* , from natural markings. *DOC Science International Series*, 191.
- Brooks, T.M. et al., 2006. Global Biodiversity Conservation Priorities. *Science*, 313, pp.58–61.
- Burnham, K.P., Anderson, D.R., White, G.C., Brownie, C. & Pollock, K.H. 1987. Design and Analysis Methods for Fish: Survival Experiments Based on Release–Recapture, 2nd edn. Monograph 5. *American Fishing Society*, Bethesda, MD.
- Caughley, G., 1994. Directions in conservation biology. *Jthe nal of Animal Ecology*, 63(2), pp.215–244.
- Choquet, Rã©. et al., 2009. U-CARE: Utilities for performing goodness of fit tests and manipulating CAPture-REcapture data. *Ecography*, 32(6), pp.1071–1074. Available at: <http://doi.wiley.com/10.1111/j.1600-0587.2009.05968.x> [Accessed September 29, 2014].
- Cincotta, R.P., Wisnewski, J. & Engelman, R., 2000. Human population in the biodiversity hotspots. *Nature*, 404(April), pp.25–27.
- Colding, J., 2007. “Ecological land-use complementation” for building resilience in urban ecosystems. *Landscape and Urban Planning*, 81(1-2), pp.46–55. Available at: <http://linkinghub.elsevier.com/retrieve/pii/S0169204606002179> [Accessed July 9, 2014].
- Cooch, E.G. & White, G.C., 2014. *Program MARK - A Gentle Introduction (13th edition)*,
- Cowling, R.. et al., 2003. A conservation plan for a global biodiversity hotspot—the Cape Floristic Region, South Africa. *Biological Conservation*, 112(1-2), pp.191–216. Available at: <http://linkinghub.elsevier.com/retrieve/pii/S0006320702004251> [Accessed July 16, 2014].
- Cressey, E.R., Measey, G.J. & Tolley, K. a., 2014. Fading out of view: the enigmatic decline of Rose's mountain toad *Capensibufo rosei*. *Oryx*, (February 2013), pp.1–8. Available at: [http://www.jthe nals.cambridge.org/abstract\\_S0030605313001051](http://www.jthe nals.cambridge.org/abstract_S0030605313001051) [Accessed July 31, 2014].
- Fairchild, L., 1984. Male Reproductive Tactics in an Explosive Breeding Toad Population. *American Zoologist*, 24(2), pp.407–418.
- Foin, T.C. et al., 1998. Recovery Planning for Threatened and Endangered Species. *BioScience*, 48(3), pp.177–184.
- Forsyth, G.G. & Wilgen, B.W.V.A.N., 1998. The recent fire history of the Table Mountain National Park and implications for fire management. *Koedoe*, 50(1), pp.3–9.
- Gamble, L., Ravela, S. & McGarigal, K., 2007. Multi-scale features for identifying individuals in large biological databases: an application of pattern recognition technology to the marbled salamander

Ambystoma opacum. *Journal of Applied Ecology*, 45(1), pp.170–180. Available at: <http://doi.wiley.com/10.1111/j.1365-2664.2007.01368.x> [Accessed September 20, 2014].

Garris, A.J. et al., 2005. Genetic structure and diversity in *Oryza sativa* L. *Genetics*, 169(3), pp.1631–8. Available at: <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1449546&tool=pmcentrez&rendertype=abstract> [Accessed July 14, 2014].

Griffiths, R. a., Sewell, D. & McCrea, R.S., 2010. Dynamics of a declining amphibian metapopulation: Survival, dispersal and the impact of climate. *Biological Conservation*, 143(2), pp.485–491. Available at: <http://linkinghub.elsevier.com/retrieve/pii/S0006320709004820> [Accessed October 6, 2014].

Grumbine, R.E., 1994. What Is Ecosystem Management ? *Conservation Biology*, 8(1), pp.27–38.

Hazell, D., Osborne, W. & Lindenmayer, D., 2003. Impact of post-European stream change on frog habitat: southeastern Australia. *Biodiversity and Conservation*, 12, pp.301–320.

Hof, C. et al., 2011. Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature*, 480(7378), pp.516–9. Available at: <http://www.ncbi.nlm.nih.gov/pubmed/22089134> [Accessed July 14, 2014].

Hyten, D.L. et al., 2006. Impacts of genetic bottlenecks on soybean genome diversity. *Proceedings of the National Academy of Sciences of the United States of America*, 103(45), pp.16666–71. Available at: <http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=1624862&tool=pmcentrez&rendertype=abstract>.

IUCN, 2004. Global Amphibian Assessment. *Conservation International Centre for Applied Biodiversity Science, NatureServe, IUCN Global Amphibian Assessment*.

Kremen, C., Merenlender, A.M. & Murphy, D.D., 1994. Ecological Monitoring : Conservation Need for Integrated in Programs and Development the Tropics. *Conservation Biology*, 8(2), pp.388–397.

Liley, D. & Clarke, R.T., 2003. The impact of urban development and human disturbance on the numbers of nightjar *Caprimulgus europaeus* on heathlands in Dorset, England. *Biological Conservation*, 114, pp.219–230. Available at: <http://linkinghub.elsevier.com/retrieve/pii/S0006320703000429> [Accessed September 17, 2014].

McKinney, M.L., 2002. Urbanization, Biodiversity, and Conservation. *BioScience*, 52(10), pp.883–890.

Measey, G.J., 2011. *Ensuring a future for South Africa's frogs: a strategy for conservation research*,

Mittermeier, R.A. et al., 1998. Biodiversity Areas : Hotspots to and Setting Major Tropical Conservation Wilderness Priorities Approaches. *Conservation Biology*, 12(3), pp.516–520.

- Morrison, C., Hero, J. & Browning, J., 2004. Herpetologists' League Altitudinal Variation in the Age at Maturity, Longevity, and Reproductive Lifespan of Anurans in Subtropical Queensland. *Herpetologia*, 60(1), pp.34–44.
- Myers, N., 1990. The biodiversity challenge: Expanded hot-spots analysis. *The Environmentalist*, 10(4), pp.243–256. Available at: <http://link.springer.com/10.1007/BF02239720>.
- Nichols, J.D. et al., 2014. Estimation of Contributions to Population Growth: A Reverse-Time Capture-Recapture Approach. *Ecology*, 81(12), pp.3362–3376.
- Page, R.D.M., & E.C. Holmes. 1998. Molecular evolution: A phylogenetic approach. Blackwell Publishing, Oxford, United Kingdom.
- Parrish, J.D., David, P. & Unnasch, R.S., 2003. Are I Conserving What I Say I Are? Measuring Ecological Integrity within Protected Areas. *BioScience*, 53(9).
- Pianka, E.R., 1970. On r- and K-selection. *The American Naturalist*, 104(940), pp.592–597.
- Pike, D.A. et al., 2008. Estimating Survival Rates of Uncatchable Animals: The Myth of High Juvenile Mortality in Reptiles. *Ecology*, 89(3), pp.607–611.
- R Core Team. 2013. R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria*. URL <http://www.R-project.org/>.
- Rannally, L.A.A.B., Erger, L.E.E.B. & Kerratt, L.F.S., 2013. Comparison of three widely used marking techniques for adult anuran species *Litoria verreauxii* aplina. *Herpetological Conservation and Biology*, 9(2), pp.428–435.
- Richardson, D.M. et al., 1996. Current and future threats to plant biodiversity on the Cape Peninsula, South Africa. *Biodiversity and Conservation*, 5, pp.607–647.
- SANParks 2004, South Africa, viewed 31 October 2014.  
<[www.sanparks.co.za/parks/table\\_mountain/about/history.php](http://www.sanparks.co.za/parks/table_mountain/about/history.php)>
- Skalski, J. R., A. Hoffmann, and S. G. Smith. 1993. Testing the significance of individual-and cohort-level covariates in animal survival studies. *Marked individuals in the study of bird population*, 1993, pp.9-28.
- Sauvajot, R.M. et al., 1998. Patterns of human disturbance and response by small mammals and birds in chaparral near urban development. *Urban Ecosystems*, 2, pp.279–297.
- Schmidt, B.R., Schaub, M. & Anholt, B.R., 2002. Why you should use capture-recapture methods when estimating survival and breeding probabilities: on bias, temporary emigration, overdispersion, and common toads. *Amphibia-Reptilia*, 23, pp.375–388.
- Shiroye, L.J. et al., 1997. Validation Tests of an Amphibian Call Count Survey Technique in Ontario, Canada. *Herpetologia*, 53(3), pp.312–320.



- Stuart, S.N. et al., 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* (New York, N.Y.), 306(5702), pp.1783–6. Available at: <http://www.ncbi.nlm.nih.gov/pubmed/15486254> [Accessed July 14, 2014].
- Stuart S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman, and R. W. Waller. 2004. Status and trends of amphibian declines and extinctions Worldwide. *Science*, 309, pp.1783–1786.
- Tetens O. 1930. Über einige meteorologische Begriffe. *Z Geophysics*, 6 pp.279-209
- Tolley, K.A. et al., 2010. Isolation and high genetic diversity in dwarf mountain toads (*Capensibufo*) from South Africa. *Biological Journal of the Linnean Society*, 100, pp.822–834.
- Turner, A.A. & de Villiers, A.L., 2007. Chapter 4: Amphibians. In *Cape Nature, Western Cape State of Biodiversity*. pp. 36–54.
- Wagner, W.E., Sullivan, B.K. & Wagner, E., 1992. Chorus Organization in the Gulf Coast Toad (*Bufo valliceps*): Male and Female Behavior and the Opportunity for Sexual Selection. *Copeia*, 1992(3), pp.647–658.
- Wells, K.D., 1979. Reproductive Behavior and Male Mating Success in a Neotropical Toad, *Bufo typhonius*. *Biotropica*, 11(4), pp.301–307.
- Welsh, H.H. & Ollivier, L.M., 1998. Stream Amphibians as Indicators of Ecosystem Stress: A Case Study from California's Redwoods. *Ecological Applications*, 8(4), pp.1118–1132.
- White, G.C. & Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study*, 46(sup001), pp.S120–S139. Available at: <http://www.tandfonline.com/doi/abs/10.1080/00063659909477239>.
- Van Wilgen, B.W. et al., 2008. A biome-scale assessment of the impact of invasive alien plants on ecosystem services in South Africa. *Journal of environmental management*, 89(4), pp.336–49. Available at: <http://www.ncbi.nlm.nih.gov/pubmed/17765388> [Accessed September 16, 2014].
- Van Wilgen, B.W. et al., 2010. Fire management in Mediterranean-climate shrublands: a case study from the Cape fynbos, South Africa. *Journal of Applied Ecology*, 47(3), pp.631–638. Available at: <http://doi.wiley.com/10.1111/j.1365-2664.2010.01800.x> [Accessed August 26, 2014].
- Wilgen, B.W. Van, Forsyth, G.G. & Prins, P., 2012. The Management of Fire-Adapted Ecosystems in an Urban Setting: the Case of Table Mountain National Park, South Africa. *Ecology and Society*, 17(1).
- Woolbright, L.L., 1983. Sexual Selection and Size Dimorphism in Anuran Amphibia. *The American Naturalist*, 121(1), pp.110–119.
- Xu, C.Y. & Singh, V.P., 1998. Dependence of evaporation on meteorological variables at different time-scales and intercomparison of estimation methods. *Hydrological process*, 12, pp.429–442.

